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COVER IMAGES

FRONT COVER: Figure 5 in Kavanaugh et al., Dorsal habitus of *Omophron* species.
A. *O. pseudotestudo* Tian & Deuve (CASENT1012671; Longchuan Jiang, Wuhe Township, Tengchong County, Yunnan, China); B. *O. pseudotestudo* (Paratype; Jianhong, Xishuangbanna, Yunnan, China).

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Benthic Heterobranch Sea Slugs (Gastropoda: Heterobranchia) from Santa Barbara County, California. II. Tar Pits Reef, Carpinteria, 2008–2020

Jeffrey H. R. Goddard ¹, Zygmund E. Goddard ², William M. Goddard ²

¹ Marine Science Institute, University of California, Santa Barbara, CA 93106-6150; email: jeffg@ucsb.edu. ² Midland School, 5100 Figueroa Mountain Rd., Los Olivos, CA 93441

From 2008 to 2020 we sampled the rocky intertidal at the southeast end of Carpinteria State Beach 40 times for benthic heterobranch sea slugs, recording a total of 3590 individuals from 52 species, 45 of which were nudibranchs. The aeolid nudibranch *Flabellinopsis iodinea* was the most frequently encountered species, followed by *Orienthella trilineata*, *Hermissenda opalescens*, *Dendronotus venustus*, and *Doto* form A of Goddard (1996). These five species, four of which prey exclusively on hydrozoans, along with two herbivorous species (the bubble snail *Haminoea virescens* and the sea hare *Aplysia californica*) were also the most abundant species. Nudibranchs specializing on sea anemones were rare. Southern species, with primarily Californian or Panamic biogeographic affinities, dominated the heterobranch assemblage at Tar Pits Reef with 35 species, and their prevalence relative to the nine total northern species generally tracked the El Niño Southern Oscillation as measured by the Multivariate ENSO Index. During the strong 2015–16 El Niño the three most abundant northern species (*Doto columbiana*, *Dendronotus subramosus*, and *Doris montereyensis*) were absent from Tar Pits Reef, while conspicuous southern species, including *Thordisa bimaculata*, *Doriopsilla gemela*, *F. iodinea*, and *Limacia mcdonaldi*, peaked in abundance. Tar Pits Reef remains the only intertidal locality known for the aeolid nudibranch *Pacifia goddardi* and one of only three localities known for *Janolus anulatus* in California outside of San Diego.

The mainland shore of southern Santa Barbara County is dominated by sandy beaches and stretches of seaward-dipping sedimentary bedrock subject to seasonal inundation by sand (Dibblee 1950; Dugan et al. 2000; personal observations). Boulder fields punctuate the shoreline near the mouths of coastal streams. Heterobranch sea slugs (hereafter, heterobranchs), particularly herbivorous bubble snails and sea hares and fast-growing, hydroid-feeding cladobranchs, occur in these rocky habitats. However, frequent inundation by sand and overturning of boulders by storm waves suppress the development of the lush encrusting biota capable of supporting species-rich assemblages of heterobranchs —especially nudibranchs— found in less physically disturbed, wave-protected outer-coast rocky shores more common north of Point Conception (Ricketts et al. 1985; Littler et al. 1991; and see for example Nybakken 1978; Goddard 1984).

Over the past 20 years we have found only two intertidal sites rich in species of nudibranchs from Gaviota east through Santa Barbara and Ventura Counties: Naples Point, the heterobranch fauna of which was documented by Goddard et al. (2020), and Tar Pits Reef, Carpinteria (hereafter, Tar Pits), the subject of the present paper. The broad intertidal bench and rocky outcrops at Coal Oil Point near Isla Vista might initially appear promising, but have few overhanging ledges in the

low intertidal, are subject to extensive seasonal inundation by sand (Littler et al. 1991; personal observations), and therefore unable to support diverse heterobranch assemblages.

The first heterobranch gastropod recorded from Carpinteria was the large and conspicuous aeolid nudibranch *Phidiana iodinea* (Cooper, 1863) (= *Flabellinopsis iodinea*) Yates (1890). This was also the first species observed by the senior author at Tar Pits in June 1973, and again in November 1998 (JG, personal observations), anticipating our finding in the present study that *F. iodinea* was the most frequently observed heterobranch at this site. Sphon and Lance (1968) listed *F. iodinea* and 12 other species of heterobranchs from Carpinteria. One of these, *Onchidoris hystricina* (non Bergh, 1878 = *Diaphorodoris lirulatocauda* Millen, 1985), was noted as occurring at 15' depth, and therefore may have been from Carpinteria Reef, a well-known dive site located in shallow water off Sand Point, 2 km northwest of Tar Pits Reef (Fig. 1). Lee and Brophy (1969) listed *Acanthodoris atrogriseata* O'Donoghue, 1927 from "Serena Cove, Carpinteria," which is located inside Loon Point 6.2 km northwest of Tar Pits. Gosliner (2010) described *Flabellina goddardi* (= *Pacifia goddardi*) based on a single specimen from Tar Pits, where it has since been found regularly on the undersides of ledges in the spring and early summer (Goddard and Hoover 2016). Goddard et al. (2016) extended the known range of *Janolus anulatus* Camacho-Garcia and Gosliner, 2006 to Tar Pits and also reported the occurrence at that site of *Thordisa bimaculata* Lance, 1966 and *Doriopsilla gemela* Gosliner, Schaefer and Millen, 1999.

Here, we document heterobranchs from the intertidal zone at Tar Pits based on our 12 years of observations. We present data on the frequency of occurrence for 52 total species, describe seasonal patterns of occurrence and egg-laying for the most abundant species, and discuss the composition of the assemblage in relation to the occurrence of their prey species at Tar Pits. Following Goddard et al. (2020) we also document changes in the abundance of southern versus northern species associated with the El Niño Southern Oscillation (ENSO) and the onset of the strong marine heat waves observed in the Northeast Pacific Ocean in 2014 (Sanford et al. 2019).

STUDY SITE

Tar Pits Reef (34.3869, -119.5165) is a small sedimentary rock bench located at the southeast end of Carpinteria State Beach, 2 km southeast of Sand Point and 4 km northwest of Rincon Point (Fig. 1). When exposed on minus tides, the bench measures approximately 40 m in breadth, extends seaward approximately 70 m, and is cut by shallow channels and pocketed with scattered pools and short undercut ledges (Fig. 2). Landward it is backed by a sandy beach approximately 65 m wide, and behind that a marine terrace 2 m high fronted by sandstone rip rap and natural outcrops of asphalt (giving the reef its name). Parallel elevated ridges on the seaward edge of the bench run east-west and on minus tides not only block the inner reef from waves, but also harbor a set of productive tide pools, including one 26 m long x 1 m wide, and up to 1 m deep (Fig. 2B). The site as a whole is fairly wave-exposed, and cobbles are absent on the bench except at the bottom of a few deeper tide pools. Sand levels on the adjacent beach build through the summer, inundating the landward edge of the bench and most of its shallow channels, but then decline in winter, exposing underlying bedrock, cobble, and an old, city drainpipe spanning the beach. The tallest outcrop on the bench is approximately 2 m high, located on the landward edge of the bench, and forms an overhanging ledge with a shallow cave accessible on minus tides when sand levels are low. Vertical rock walls near the seaward edge of the bench reach heights of 2 m; otherwise, vertical relief on the bench is under 1 m. Sandy beaches extend 5.5 km northwest to Loon Point (broken only at Sand Point by the narrow entrance to the Carpinteria estuary) and 4 km southeast to the intertidal boulder field at Rincon Point.

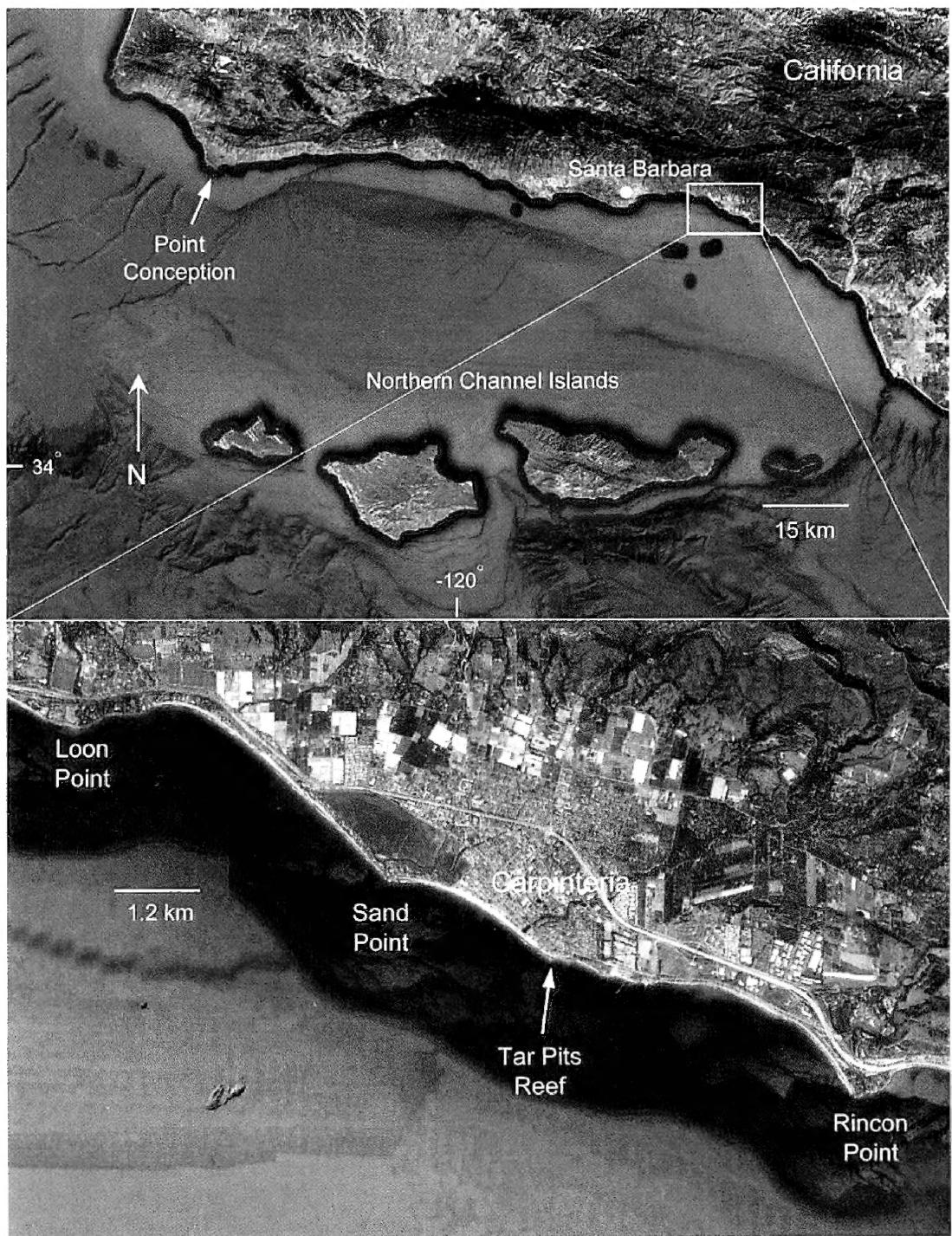


FIGURE 1. Map of southern Santa Barbara County showing location of Carpinteria and Tar Pits Reef.

A



B



FIGURE 2. Tar Pits Reef study site, 20 May 2011, on a -0.3 m tide. (A) Overview of reef, looking south from Carpinteria beach. (B) Looking northwest from near the seaward end of the reef. The pool at left center measures 26 m long x 1 m wide. Carpinteria State Beach and Santa Ynez Mountains visible at upper right.

Higher portions of the reef are dominated by mussels *Mytilus californianus* Conrad, 1837, goose barnacles *Pollicipes polymerus* Sowerby, 1833, acorn barnacles, and limpets *Lottia* spp., while lower portions are dominated by surfgrass *Phyllospadix torreyi* S. Watson, 1879 interspersed with sunburst anemones *Anthopleura sola* Pearse and Francis, 2000. Feather-boa kelp *Egregia menziesii* (Turner) Areschoug, 1876 is prevalent in pools on the lower bench. Two-spot octopuses, Pacific rock crab *Romaleon antennarium* (Stimpson, 1856), and common ochre stars *Pisaster ochraceous* (Brandt, 1835) are among the more conspicuous and prevalent invertebrate predators on the reef. Pacific harbor seals *Phoca vitulina* Linnaeus, 1758 regularly haul out on the seaward portions of the reef.

Human visitation during low tides at the Tar Pits is high, primarily by local residents, school groups, and families camping at Carpinteria State Park. Since 1992 the reef has also been monitored by the Multi-Agency Rocky Intertidal Network (MARINe), which targets common, primarily sessile benthic organisms, including anemones (*Anthopleura* spp.), acorn and goose barnacles (*Balanus* spp., *Chthamalus* spp., and *Pollicipes polymerus*), mussels (*Mytilus* spp.), surfgrass (*Phyllospadix* spp.), and common ochre stars (*Pisaster ochraceous*) (<<https://marine.ucsc.edu/sitepages/carpinteria.html>>). MARINe has also conducted three biodiversity surveys at Carpinteria (in 2001, 2012, and 2019), recording among 257 total taxa a single species of heterobranch, *Hermisenda crassicornis* (Eschscholtz, 1831) (= *H. opalescens* (Cooper, 1863) in southern California) (<<https://marine.ucsc.edu/sitepages/carpinteria-bio.html>>; R. Gaddam, personal communication to JG, 19 Dec 2019).

METHODS

On low tides falling below -0.2 m and occurring between dawn and dusk, we searched low intertidal pools, walls, and under ledges for heterobranchs. In low light situations, such as shaded habitat or prior to sunrise, we used dive lights to illuminate our field of search. On each trip we recorded the number of individuals of each species found and the presence of their egg masses. For species reaching high densities, we counted all individuals encountered when sparse, but when their numbers were high we subjectively estimated minimum abundance by fives or order of magnitude. These values were entered in Excel as the order of magnitude plus one (e.g., 26 for 25, 101 for 100). For each sampling trip we also noted the time spent searching and the number of observers. For larger species the senior author frequently recorded individual size as simply small, medium, or large, with these categories based on the author's prior experience with those species. Where presented below, these size categories are defined for individual species. Counts of individuals by species, presence/absence of their egg masses, and search time for each of our sampling trips can be obtained from Goddard (2020).

During the early years of this study we took photographs only of rare or unusual species, or species whose mode of development the senior author was examining. However, beginning in 2014, and using a Pentax WG III waterproof camera, we endeavored to photograph all species encountered, and sometimes each species found on each sampling trip. Since 2017 we have posted these images on the online database iNaturalist (<https://www.inaturalist.org>). Observations on iNaturalist mentioned below are referenced by their unique observation numbers (e.g., iNaturalist 22910457).

We sampled Tar Pits 40 times from May 2008 to June 2020, averaging 2.8 monthly visits per year (SD = 1.6, range 1 – 7 months per year). Across all years sampled we did not sample in February or September, and we sampled the remaining 10 calendar months from 1 to 10 times each (Mean = 3.6, SD = 2.8). We sampled most frequently in the spring (n = 21 months; defined as April through June), followed by winter (n = 7; defined as January through March), fall (n = 5), and summer (n = 3). We sampled May 2014 and August 2019 each twice and May 2018 three times; for data summaries and analyses, the counts of species and individuals within these months were combined and treated as one, as were the total number of hours searched per observer.

Owing to the relatively low frequency of our sampling we utilize two types of time series in presenting results: (1) by season, averaging the monthly data in each season across all years sampled, and (2) by year, averaged across all months sampled each year. Changes in abundance are standardized as number of individuals found per hour per observer. Unless specified otherwise, counts of individuals recorded and used in these analyses were by JG; counts of the number of species present were by all observers combined.

Incidental to our survey of heterobranchs we obtained information on their prey at Tar Pits. Prey species were determined by observations in the field of close association of adult slugs and potential prey, and direct observations in either the field or lab of feeding activity. Prey were identified to the lowest possible taxon using Carlton (2007).

Ranges and oceanographic indices

We assigned each species to a geographic range group as follows: (1) northern species as those ranging south only to San Diego or northern Baja California and northward to at least central Oregon, (2) southern species as those ranging south to at least Baja California Sur and northward usually only to southern, central, or northern California, and (3) widespread species as those ranging from at least as far south as Baja California Sur and at least as far north as Washington. By this classification northern species are primarily from the Oregonian Biogeographic Province, and southern species are mainly from the Panamic or Californian Provinces. We tallied the number of species in each range group found each month and then converted those counts to proportions by dividing them by the total number of species found in each range group over the entire study. Because we did not sample every month or even every season in each year, we averaged these monthly proportions by year and then compared their changes over time to fluctuations in the Multivariate ENSO Index (MEI) (MEI.v2, NOAA Earth System Research Laboratory, available from: <https://www.esrl.noaa.gov/psd/enso/mei/>), the bimonthly values of which we also averaged by year.

RESULTS

Species composition and abundance

In 40 total trips to Tar Pits from 2008 to mid-2020 we recorded 3590 individual heterobranchs in 52 species (Table 1). These included 45 species of nudibranchs, 3 cephalaspideans, 2 aplysiids, and 2 sacoglossans. Eight species, representative of three of these taxa, as well as prevalent dietary preferences at Tar Pits (see below), are shown in Figure 3. The nudibranch *Dendronotus venustus* MacFarland, 1966, was the most abundant species, followed by the Green bubble snail *Haminoea virescens* (Sowerby, 1833) (Fig. 3A), the aeolid nudibranchs *Hermissenda opalescens*, *Flabellinopsis iodinea* (Fig. 3G), and *Orienthella trilineata* (O'Donoghue, 1921), the sea hare *Aplysia californica* (Cooper, 1863), and the nudibranchs *Doto* form A of Goddard (1996), *Dirona picta* MacFarland, 1905, *Doriopsilla albopunctata* (Cooper, 1863), and *Doto columbiana* O'Donoghue, 1921. *Flabellinopsis iodinea*, found in 75% of the 36 total months sampled, was the most frequently encountered species, followed closely by *Orienthella trilineata*, at 72%. Fifteen species were found only during single months, and all but two of these (*Ancula pacifica* MacFarland, 1905, and *Geitodoris heathi* (MacFarland, 1905)) were represented by single specimens. Southern species, as defined above, dominated the assemblage at 35 species, followed by 9 northern species, and 8 widespread species (Table 1).

Voucher specimens of seven species of nudibranchs were collected during this study (see Appendix).

Images were obtained of 37 of the 52 heterobranch species recorded at Tar Pits and can be found in the senior author's observations on iNaturalist (<https://www.inaturalist.org/observations/jeffgoddard>) by searching (all fields) for "Carpinteria" and under taxon for "Heterobranch Gastropods".

The cumulative number of species we found at Tar Pits climbed steadily through 2015, leveled off at 48 species starting in 2017, and then increased by two species in mid-2019 and two more in mid-2020 (Fig. 4).

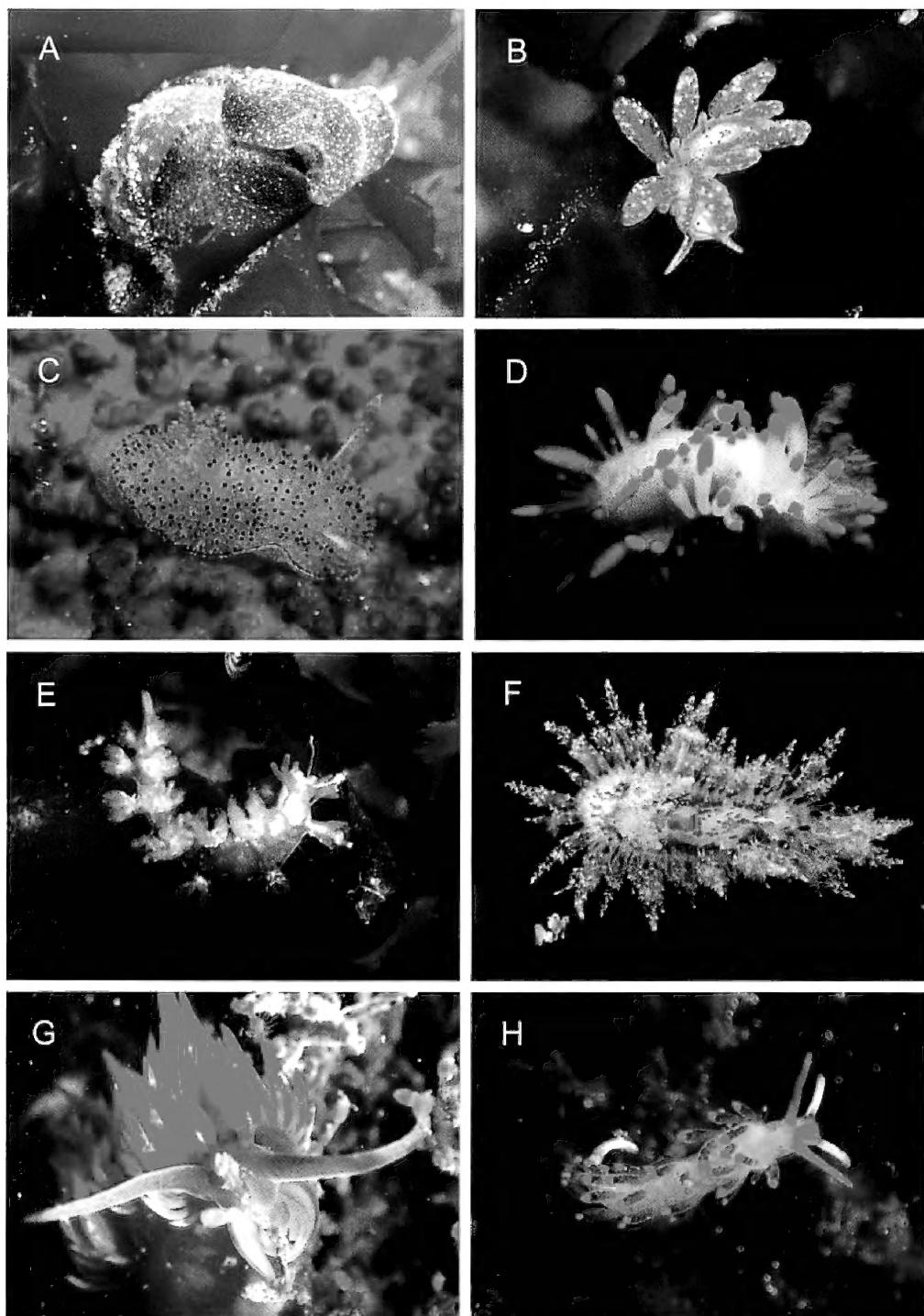


FIGURE 3. Selected heterobranch sea slugs found at Tar Pits Reef during the present study. (A) *Haminoea virescens*, 18 June 2019. (B) *Stiliger fuscovittatus*, 22 August 2017. (C) *Acanthodoris rhodoceras*, 30 April 2017. (D) *Limacia medondi*, 2 August 2019. (E) *Hancockia californica*, 31 August 2019. (F) *Janolus amulatus*, 22 August 2017. (G) *Flabellinopsis iodinea* feeding on *Eudendrium cf. ramosum*, 31 January 2018. (H) *Diaphoreolis lagunae*, 18 May 2018.

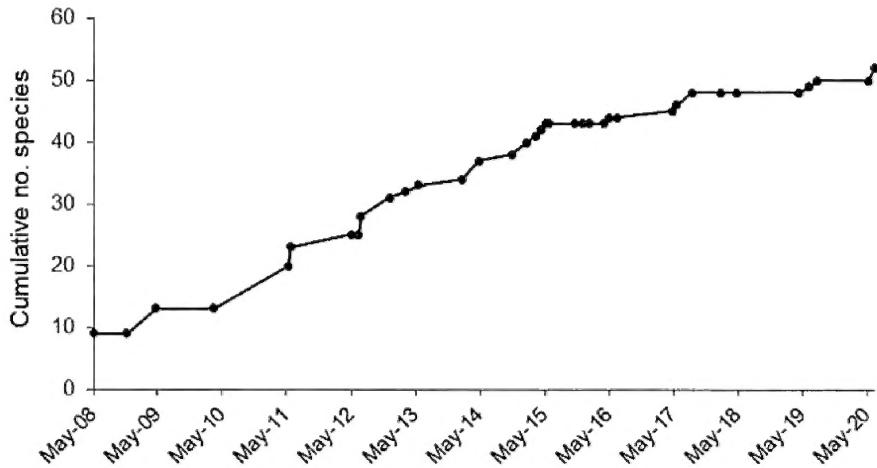


FIGURE 4. Cumulative number of species of heterobranchs found at Tar Pits Reef, Carpinteria, 2008–20.

Prey

We obtained information on the prey of 23 species of heterobranchs at Tar Pits Reef (Table 1). Specialists included the cladobranchs *Dendronotus subramosus* MacFarland, 1966, *Doto columbiana*, *Diaphoreolis lagunae* (O'Donoghue, 1926), *Flabellinopsis iodinea*, *Orientella trilineata*, and *Pacifia goddardi* on single species of hydrozoans, and *Tritonia festiva* (Stearns, 1873), and *T. myrakeenae* Bertsch and Mozqueira, 1986, on a common but undescribed stoloniferous clavulariid octocoral. *Janolus anulatus* specialized on *Synnotum aegyptiacum* (Audouin, 1826), an arborescent bryozoan on which it was strikingly well camouflaged (iNaturalist 2940672, 2nd and 3rd images). Perennial colonies of *Eudendrium* cf. *ramosum* (Linnaeus, 1758), the prey of *F. iodinea*, were abundant along the walls of surge channels and near the water line of low intertidal pools extending under ledges at Tar Pits Reef, with new polyps especially apparent in fall, after storm waves had removed sand that had built up late spring and summer.

Seasonality and egg-laying

We observed an average of 11.6 species of heterobranchs per month (Range = 1–27 species, $n = 36$). Averaged by season the total number of species found per month was highest in spring and summer (14.7 and 13.7 species, respectively; Fig. 5A) and lowest in fall and winter (4.0 and 7.0 species, respectively). The number of individuals of nudibranchs at Tar Pits we found each season ranged from 6.2 to inds. h^{-1} observer $^{-1}$ in fall to 39.7 inds. h^{-1} observer $^{-1}$ in spring (Fig. 5B), with a grand mean of 28.8 inds. h^{-1} observer $^{-1}$ ($n = 4$ seasons).

The 10 most abundant species observed in this study exhibited seasonal changes in abundance and fell into two groups: those tending to peak in spring or summer (Figure 6A–E), and those tending to peak in winter or fall and winter (Figure 6F–J). The former group included the three most abundant species we observed (*Dendronotus venustus*, *Haminoea virescens*, and *Hermisenda opalescens*), and the latter included the next three most abundant species (*Flabellinopsis iodinea*, *Orientella trilineata*, and *Aplysia californica*).

We observed egg masses of 20 species of heterobranchs at Tar Pits (Table 2). Egg masses of *Polycera atra* MacFarland, 1905, were observed in all seasons, followed by *Flabellinopsis iodinea*,

Table 1. Heterobranch sea slugs from Tar Pits Reef, 2008–20. Frequency of occurrence calculated from number of months found out of 36 total months sampled.

Species	Total No. Inds.	Freq. Occur. (%)	Geog. Range	Prey at Tar Pits Reef
<i>Flabellinopsis iodinea</i>	274	75	S	<i>Eudendrium cf. ramosum</i>
<i>Orienthella trilineata</i>	232	72.2	S	Corynidae
<i>Hermisenda opalescens</i>	554	69.4	S	
<i>Doto form A of Goddard</i>	154	63.9	S	Campanulariidae
<i>Dendronotus venustus</i>	864	63.9	W	Campanulariidae
<i>Polycera atra</i>	64	55.6	S	<i>Bugula neritina</i>
<i>Tritonia myrakeenae</i>	51	55.6	S	Clavulariidae
<i>Doriopsilla albopunctata</i>	74	52.8	S	
<i>Aplysia californica</i>	158	41.7	S	
<i>Diadula sandiegensis</i>	35	41.7	S	Chalinidae
<i>Dirona picta</i>	79	38.9	S	Ceiliostomata
<i>Pacifia goddardi</i>	62	36.1	S	<i>Bougainvillia</i> -like sp. B of Goddard and Hoover (2016)
<i>Limacia mcdonaldi</i>	44	33.3	S	
<i>Haminoea virescens</i>	590	33.3	W	
<i>Doto columbiana</i>	69	30.6	N	<i>Aglaophenia</i> sp.
<i>Diaphoreolis lagunae</i>	23	27.8	S	<i>Xingyurella turgida</i>
<i>Hancockia californica</i>	41	27.8	S	Campanulariidae
<i>Orienthella cooperi</i>	18	27.8	S	Corynidae
<i>Acanthodoris rhodoceras</i>	29	22.2	S	<i>Alcyonium</i> sp.
<i>Janolus anulatus</i>	27	22.2	S	<i>Synnotum aegyptiacum</i>
<i>Dendronotus subramosus</i>	11	19.4	N	<i>Aglaophenia</i> sp.
<i>Doris montereyensis</i>	15	19.4	N	
<i>Thordisa bimaculata</i>	13	19.4	S	
<i>Aplysia vaccaria</i>	6	16.7	S	
<i>Triopha maculata</i>	14	16.7	S	Bryozoa
<i>Corambe pacifica</i>	11	16.7	W	<i>Membranipora</i> sp.
<i>Aeolidia loui</i>	8	13.9	S	
<i>Rostanga pulchra</i>	6	13.9	W	Red orange Poecilosclerida
<i>Diaphorodoris lirulatocauda</i>	4	11.1	N	
<i>Doriopsilla gemela</i>	8	11.1	S	
<i>Navanax inermis</i>	9	11.1	S	<i>Haminoea virescens</i>
<i>Tritonia festiva</i>	4	8.3	N	Clavulariidae
<i>Aegires albopunctatus</i>	4	8.3	W	
<i>Eubranchus rustyus</i>	3	8.3	W	<i>Plumularia</i> sp.
<i>Trinchesia albocrusta</i>	5	8.3	W	
<i>Doto kya</i>	2	5.6	N	<i>Plumularia</i> sp.
<i>Antiochella barbarensis</i>	7	5.6	S	Ceiliostomata
<i>Catriona columbiana</i>	1	2.8	N	
<i>Geitodoris heathi</i>	2	2.8	N	
<i>Hermaea oliviae</i>	1	2.8	N	
<i>Acanthodoris lutea</i>	1	2.8	S	
<i>Aldisa sanguinea</i>	1	2.8	S	
<i>Ancula lenticinosa</i>	1	2.8	S	
<i>Ancula pacifica</i>	3	2.8	S	
<i>Antaeoelidiella chromosoma</i>	1	2.8	S	
<i>Bulla gouldiana</i>	1	2.8	S	
<i>Cadlina sparsa</i>	1	2.8	S	
<i>Flabellina</i> sp. 1	1	2.8	S	
<i>Flabellina</i> sp. 2	1	2.8	S	
<i>Okenia angelensis</i>	1	2.8	S	
<i>Phidiana hiltoni</i>	1	2.8	S	
<i>Stiliger fuscovittatus</i>	1	2.8	W	
Total No. Inds.	3590			

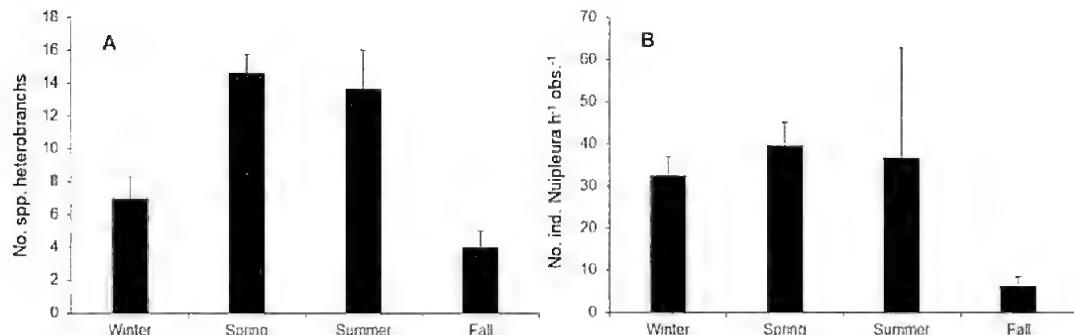


FIGURE 5. Seasonal change at Tar Pits Reef in (A) number of species of Heterobranchia and (B) number of individuals of Nudipleura found per observer per hour. Values shown are means \pm 1 SE of monthly data averaged by season across all years sampled.

Doto form A, and *Diaphula sandiegensis* (Cooper, 1863), in 3 seasons, and *Haminoea virescens*, *Hermissenda opalescens*, and *Orientella trilineata* in 2 (Table 2; Figure 6). The egg masses of the remaining 13 species were each found in only one season. As a proportion of months sampled in each season, the egg masses of most of the above species were more prevalent in some seasons than others (Table 2). For example, the eggs of *Haminoea virescens* were most prevalent in spring, those of *Polycera atra* in summer, and those of *Doto* form A in winter.

Interannual variability

The proportion of northern species exceeded that of southern species at Tar Pits Reef in 2009 and again in 2011, but from 2012 on was exceeded by the proportion of southern species, with the discrepancy climbing from 2015 on, as the El Niño Southern Oscillation peaked in 2015 and again in 2019 (Fig. 7). With a few yearly lags and leads, the prevalence of southern species tended to track the El Niño Southern Oscillation as measured by the yearly mean MEI (Fig. 7).

Coincident with the marine heat waves of 2014–2016 in the NE Pacific the three most abundant northern species of nudibranchs at Tar Pits declined in abundance to zero by 2015, while two conspicuous southern species, *Thordisa bimaculata* and *Doriopsilla gemela*, appeared for the first time and peaked in 2015 (Figs. 8A–B). Following the end of these heat waves we did not find the latter two species again, while *Flabellinopsis iodinea* and *Limacia mcdonaldi* — both of which we had observed at Tar Pits since 2010 — peaked again in 2018–19 (Fig. 8B–C). During this same period the northern species *Doto columbiana* and *Dendronotus subramosus*, but not *Doris montereyensis* Cooper, 1863, reappeared (Fig. 8A).

DISCUSSION

At Tar Pits Reef we observed 52 species of heterobranchs, 45 of which were nudibranchs, totals similar to the 55 and 48 species, respectively, we previously reported from Naples Point, located 41 km to the west (Goddard et al. 2020). The two sites shared 39 species, but as might be expected for sites differing so much in physiography (bedrock vs boulder field), their rank abundances and frequency of occurrence differed greatly, reflecting at least in part differences in availability of prey types. For example, *Dendronotus venustus*, a specialist predator of campanulariid hydroids, was the most abundant species at Tar Pits (Table 1), but at Naples Point we found only two specimens of *D. venustus* in 119 sampling trips spread over 17 years. Similarly, at Tar Pits we observed *Flabellinopsis iodinea*, a specialist predator of the hydrozoan *Eudendrium cf. ramosum*, an order of magnitude more frequently than at Naples Point. Indeed, five of the ten most abundant

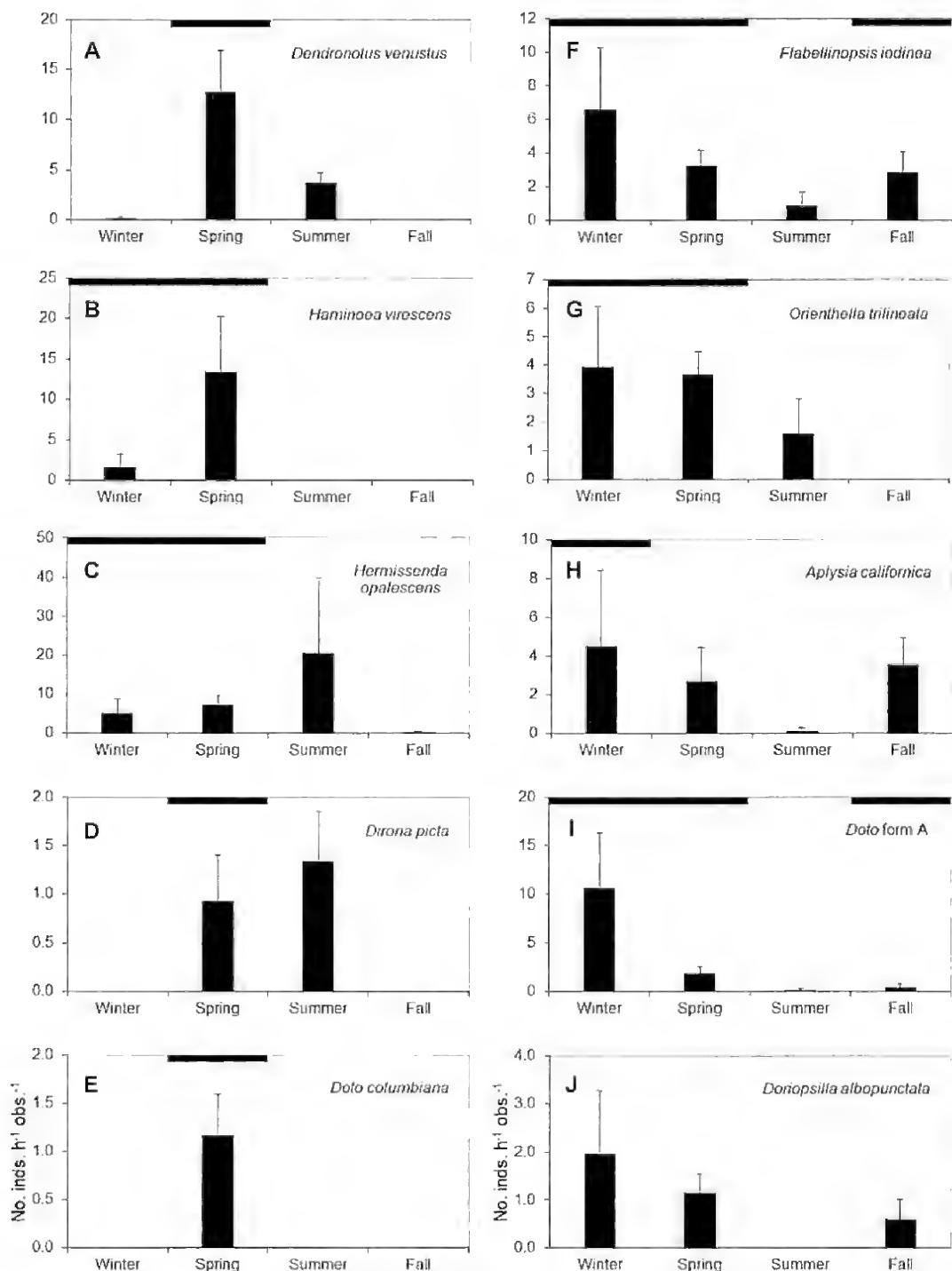


FIGURE 6. Seasonal variation in egg-laying and abundance of the 12 most abundant heterobranchs at Tar Pits Reef, 2008–20. Values shown are means ± 1 SE of monthly number of individuals per hour per observer; black bars at top of graphs indicate egg masses were observed at least once in a given season. Note that we did not observe any egg masses of *Doriopsilla albopunctata* at Tar Pits.

Table 2. Seasonal occurrence of egg masses of heterobranch gastropods at Tar Pits Reef. Values are proportions calculated as the number of times egg masses were found each season out of the total number of time each season was sampled from 2008–20, with the latter values in parentheses in the top row. Blank cells indicate values of zero.

Species	Winter (7)	Spring (21)	Summer (3)	Fall (5)
Cephalaspidea				
<i>Haminoea virescens</i>	0.14	0.43		
Anaspidea				
<i>Aplysia californica</i>	0.14			
<i>Aplysia vaccaria</i>		0.05		
Nudipleura: Doridina				
<i>Acanthodoris rhodoceras</i>		0.14		
<i>Diaulula sandiegensis</i>	0.14	0.24	0.33	
<i>Doris montereyensis</i>		0.14		
<i>Polycera atra</i>	0.14	0.43	0.67	0.2
Nudipleura: Cladobranchia				
<i>Dendronotus venustus</i>		0.29		
<i>Diaphoreolis lagunae</i>		0.05		
<i>Dirona picta</i>		0.05		
<i>Doto columbiana</i>		0.33		
<i>Doto</i> form A of Goddard (1996)	0.57	0.24		0.2
<i>Doto kya</i>		0.05		
<i>Flabellinopsis iodinea</i>	0.14	0.14		0.25
<i>Hancockia californica</i>		0.05		
<i>Hermisenda opalescens</i>	0.28	0.33		
<i>Janolus anulatus</i>		0.05		
<i>Orienthella cooperi</i>	0.14			
<i>Orienthella trilineata</i>	0.28	0.24		
<i>Pacifia goddardi</i>		0.1		

heterobranchs at Tar Pits were hydroid specialists (Table 1). In contrast, at Naples Point *Hermisenda opalescens* was the only predator of hydroids among the top ten most abundant heterobranchs, and it regularly consumes other types of prey, including ascidians, other cnidarians, and is also known to scavenge (Beeman and Williams 1980 [as *H. crassicornis*]; Megina et al. 2007 [as *H. crassicornis*]).

Similar site-specific differences in abundance emerge for nudibranchs specializing on Bryozoa and Actinaria, respectively. At Tar Pits *Dirona picta*, *Polycera atra*, and *Limacia mcdonaldi*, each of which preys exclusively on Bryozoa (McDonald and Nybakken 1997; Uribe et al. 2017), were among the 15 most abundant heterobranchs (Table 1). We did not find the latter two species at Naples Point, and only one bryozoan specialist (*Triopha maculata* MacFarland, 1905) was among the 15 most abundant species at that site (Goddard et al. 2020). Among specialists on anemones at Tar Pits we observed a total of 8 *Aeolidia loui* Kienberger, Carmona, Pola, Padula, Gosliner, and Cervera, 2016, and 1 *Antaeolidiella chromosoma* (Cockerell and Eliot, 1905). At Naples Point these totals were 54 and 334, respectively, plus 29 *Antaeolidiella oliviae* (MacFarland, 1966).

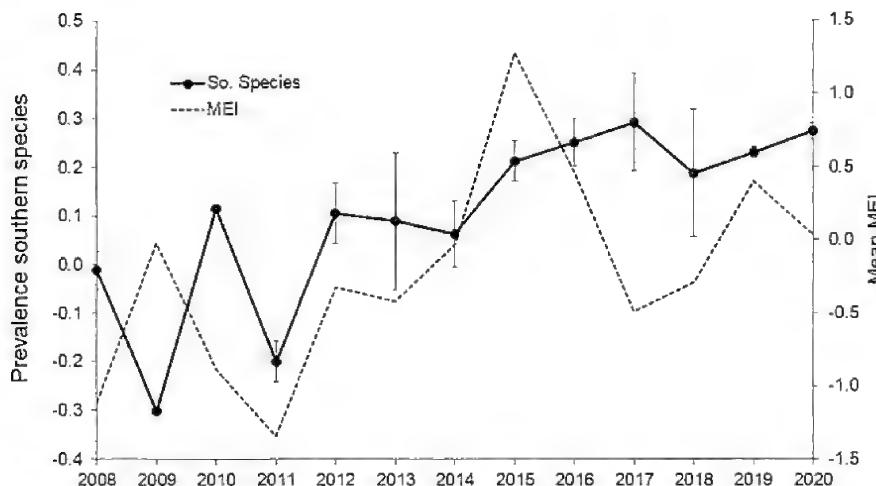


FIGURE 7. Change in relative prevalence of southern species of heterobranchs at Tar Pits Reef, with yearly mean of the Multivariate ENSO Index, 2008–20. Relative prevalence of southern species calculated as the proportion of southern species found each sample month out of the total number of southern species ($n = 35$) found throughout the entire study, minus the same proportion calculated each month for northern species. These monthly values were then averaged by year. Values shown are means ± 1 SE.

with the vast majority of individuals of all three species at that site found on the undersides of boulders near small didemnid anemones.

With more tide pools, vertical walls, and overhanging ledges, Tar Pits has more microhabitat which is shaded and open and which supports a greater abundance of hydrozoans and bryozoans compared to the tight, under-boulder habitat at Naples Point. Species such as the hydroids *Eudendrium* cf. *ramosum*, *Xingyurella turgida* (Trask, 1857), and *Aglaophenia* sp. are perennial and grow on rocky substrata or on the stipes of perennial macroalgae, while others, including many campanulariid hydroids, appear seasonally, growing epiphytically on annual algal blades and filaments. Both types of hydroids contributed to the spring/summer peaks we observed at Tar Pits in both the number of species of heterobranchs and total abundance of nudipleura (Fig. 5), as well as in the abundance of individual species (Fig. 6A–E). As sand levels build on the reef over the summer, filling pools and burying shaded habitat, and algae begin to die back in late summer, fewer sessile prey of the nudibranchs are available, contributing to the observed lows in the fall in species richness and abundance (Fig. 5). The arrival of storm waves in mid-fall begins to clear the accumulated sand, and new polyps and zooids can begin growing from perennial stolons and burial-tolerant colonies, becoming available to new recruits of nudibranchs like *Flabellinopsis iodinea*, *Orienthella trilineata*, and *Doto* form A, all of which we observed peaking in abundance in winter (Fig. 6). Consistent with fall/winter recruitment of *F. iodinea*, across all years sampled we observed small individuals (<15 mm long) from December to May, and that they were most prevalent in December and March. We did not observe any small *F. iodinea* from June through November (Fig. 9).

At Tar Pits the seasonal range in the total abundance of Nudipleura (which lacking pleurobranchs were all nudibranchs) was similar to the monthly range in abundance of nudipleurans observed by Goddard et al. (2020) at Naples Point (6.2 ind. h^{-1} obs. $^{-1}$ in fall to 39.7 in spring [Fig. 5B], compared to 7.3 in fall to 42.4 in spring at Naples). However, at Tar Pits we observed higher numbers of individuals in winter and summer, resulting in a higher grand mean at Tar Pits (28.8 ind. h^{-1} obs. $^{-1}$, compared to only 18.8 at Naples Point). Although we were measuring relative abun-

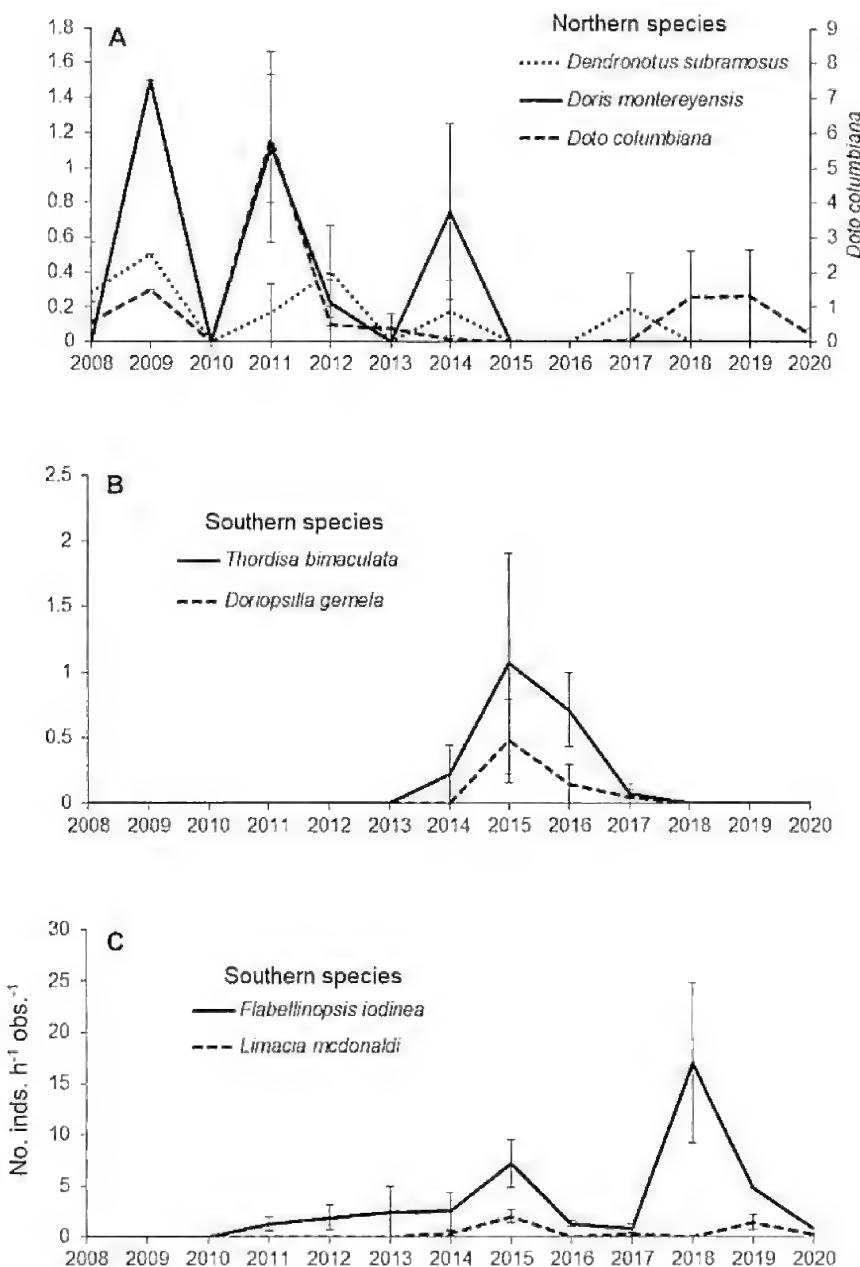


FIGURE 8. Yearly change in abundance of (A) the three most abundant northern nudibranchs at Tar Pits Reef, and (B) and (C) four southern nudibranchs at Tar Pits Reef, 2008–20. Values shown are yearly means \pm 1 SE of monthly number of individuals per hour per observer; note separate y-axis in (A) for *Doto columbiana*.

dance of heterobranchs at these sites, rather than estimating density, we suspect the total abundance of nudibranchs is even higher at Tar Pits. At Naples Point we could carefully scan the relatively two-dimensional underside of boulders for nudibranchs. Tar Pits has more caves and ledges, with walls and overhangs seasonally covered with dense, tangled mats of hydroids, bryozoans, sponges, and ascidians (see Goddard and Hoover 2016). These microhabitats can be more difficult to visually search for nudibranchs, especially in tight crevices and small caves. For example, *Tritonia myra-keenae* was the most frequently encountered nudibranch and one of the most abundant heterobranchs at Naples Point (Goddard et al. 2020). Once a search image for this diminutive nudibranch is established, both the nudibranch and its clavulariid octocoral prey are relatively easy to observe *in situ* on the undersides of boulders. The clavulariid appears to be similarly abundant at Tar Pits, but is often surrounded by other encrusting arborescent organisms, all of which can be obscured by a fine layer of silt, detritus, and associated microorganisms. In this type of microhabitat, we likely missed individuals of cryptically colored species and small species like *T. myra-keenae*.

Of the 13 species listed from Carpinteria by Sphon and Lance (1968) we found all but the sacoglossan *Elysia hedgpethi* Er. Marcus, 1961, and the dorid nudibranch *Okenia rosacea* (= *Hopkinisa rosacea* MacFarland, 1905). The senior author has observed *Bryopsis* sp., a green alga consumed by *E. hedgpethi*, in rocky intertidal pools just east of Tar Pits, so we consider the occurrence of *E. hedgpethi* at Tar Pits Reef likely, at least in some years. By contrast, we have rarely observed *Integripelta bilabiata* (Hincks, 1884), the sole known prey of *O. rosacea*, intertidally on the south coast of Santa Barbara County, and none at all within 50 km of Tar Pits Reef. The senior author has observed both *O. rosacea* and the bryozoan at Purisima Point, which is north of Point Conception and one of the other sites in Santa Barbara County listed by Sphon and Lance (1968) for *O. rosacea*. Further, Gale Sphon deposited in the Santa Museum of Natural History 6 specimens of *O. rosacea* (as *Hopkinsia rosacea*) collected from Purisima Point in December 1967 (SBMNH 25019). Without any equivalent museum records from Carpinteria, we do not know if *O. rosacea* and *I. bilabiata* used to be present at Tar Pits, or if the inclusion by Sphon and Lance (1968) of Carpinteria as one of the intertidal sites for *O. rosacea* was an error.

Acanthodoris atrogriseata, reported by Lee and Brophy (1969) from Carpinteria, California, was described from near Nanaimo, Vancouver Island, British Columbia (O'Donoghue 1927). Hallas et al. (2016) showed that specimens from Alaska identified as *A. pilosa* are actually *A. atrogriseata* and that *A. atrogriseata* is sister to the North Atlantic *A. pilosa* (Abildgaard in Müller, 1789). Because of the northern distribution of *A. atrogriseata* (limited to the Aleutian and northern Oregonian biogeographic provinces), we consider it likely that the specimen identified by Lee and Brophy (1969) as this species was likely *A. rhodoceras* Cockerell, 1905, and probably the same color form that we consistently found at Tar Pits (Fig. 3C).

Goddard and Hoover (2016) reported finding the aeolid nudibranch *Pacifia goddardi* (as *Flabellina goddardi*) at Tar Pits only during spring and summer (and mainly in May and June).

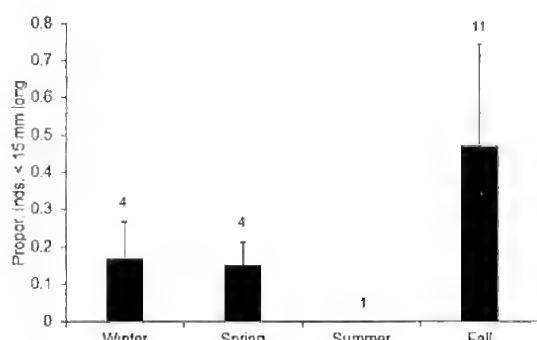


FIGURE 9. Seasonal variation in proportion of small individuals (< 15 mm long) of *Flabellinopsis iodinea* observed at Tar Pits reef, 2008–20. We found *F. iodinea* in 27/36 months sampled, but recorded size information for *F. iodinea* in only 20 of those months. Numbers above bars are sample size (= total no. months in each season during which size data were collected).

Consistent with those results, since 2016 we have found *P. goddardi* at Tar Pits only in the months of April and May. With a distribution limited to a triangle extending from Malibu to Anacapa Island to Carpinteria, *P. goddardi* has not been found at any new sites since Goddard and Hoover (2016), but it has been found subtidally throughout the year at Anacapa Island (see images by Douglas Klug here: <https://www.flickr.com/search/?text=goddard%27s%20aeolid&view_all=1>). Additionally, ZG and WG found one specimen of *P. goddardi* subtidally at Anacapa Island in August 2019 (iNaturalist 31753324). Despite careful searching at other sites in the region, including Point Dume and Latigo Point in Malibu (JG, WG, and ZG, unpublished data), Tar Pits Reef remains the only intertidal locality known for *P. goddardi*.

Unlike the southern species shown in Figure 8, the abundance of *Pacifia goddardi* at Tar Pits did not show a clear correspondence with the ENSO as measured by the mean annual MEI (Fig. 10). With such a limited geographic distribution, larval advection and the recruitment dynamics of this species at Tar Pits must more strongly reflect the regional oceanography of the mid Southern California Bight and Santa Barbara Channel and therefore likely differ from the dynamics of more widespread southern species.

Similar to the findings of Goddard et al. (2020) at Naples Point, the prevalence of southern species at Tar Pits generally tracked ENSO (Fig. 7). However, there were some striking differences in the abundance of species found at both sites. For example, at Tar Pits we observed only a single individual of the bubble snail *Bulla gouldiana* Pilsbry, 1895, compared to the sudden appearance of large numbers of this species starting in late 2015 at Naples Point (see Goddard et al. 2018, Fig. 4). Similarly, during our entire study at Tar Pits we observed a total of 6 Black sea hares *Aplysia vaccaria* Winkler, 1955; at Naples Point we observed 170 over the last 6 years of our study there (Goddard et al. 2018, Fig. 4; Goddard et al. 2020). In contrast, while we never observed the Bean clam *Donax gouldii* Dall, 1921, at Naples Point, in August 2019 we found high numbers of them on the beach at Tar Pits.

Prior to our first observation of *Janolus anulatus* at Tar Pits in May 2012, this Panamic species was known only as far north as San Diego County, where its abundance appeared to peak during four of five strong El Niño events between 1964 and 2001 (Goddard et al. 2016, Fig. 6). We expected a similar pattern to hold at its new northern range limit at Tar Pits. However, we did not find any during the marine heat waves of 2014-16, which included the very strong 2015-16 El

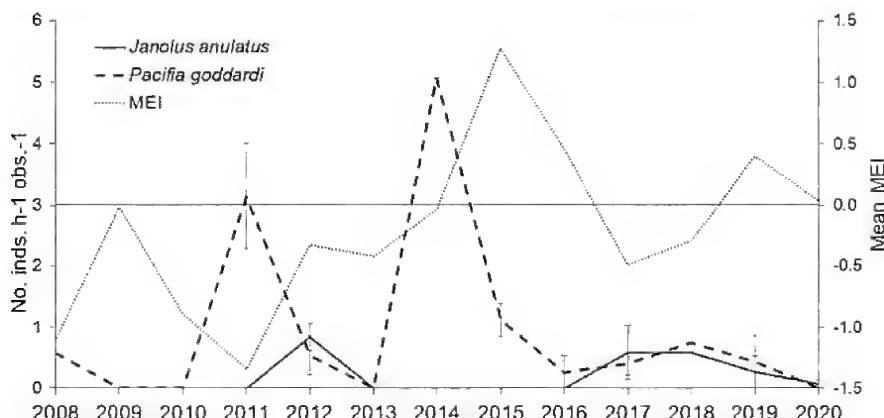


FIGURE 10. Yearly change in abundance of *Janolus anulatus* and *Pacifia goddardi* at Tar Pits Reef, with yearly mean of the Multivariate ENSO Index, 2008–20. Values shown are means \pm 1 SE of monthly number of individuals per hour per observer. The horizontal line marks a mean annual MEI = 0, above which generally indicates El Niño conditions, and below which indicates La Niña conditions.

Niño, and we next observed *J. anulatus* in 2017-18, during a weak La Niña, after which the nudibranch appeared to decrease in abundance as a weak El Niño developed in late 2018 (Fig. 10).

The reasons for the discrepancy between our results for *Janolus anulatus* from Tar Pits and those from San Diego are unclear, especially given our results for *Thordisa bimaculata* and *Doriopsilla gemela* (Fig. 8), both of which are conspicuous members of the nudibranch fauna in San Diego (personal observations). Potential local variation in recruitment dynamics aside, our time series at Tar Pits is much shorter than the nearly 40 years of data from San Diego and may not have captured a similar fluctuation in abundance. Further, one of our data points from Tar Pits raises the possibility that we did not accurately sample variation in abundance of *J. anulatus*, which as mentioned above is highly cryptic on its bryozoan prey. On 22 August 2017 we found 11 specimens, an order of magnitude more than on our other sampling trips. On that trip, owing to the pre-dawn low tide, we started searching earlier and found most of the *J. anulatus* before dawn, actively crawling out in the open on algae in tide pools. This is consistent with how this species (as well as the highest species richness of nudibranchs) has been found intertidally in La Jolla: by searching pools before dawn in late spring and summer (Jerry Jacobs and Jeff Hamann, personal communications to JHRG, and see field accounts in the James R. Lance collection at CAS). By sunrise in La Jolla the vast majority of nudibranchs have retreated under ledges and into the cover of macroalgae and epibionts lining the sides of the tide pools and are no longer visible (personal observations). This diel behavior, which the senior author has not observed intertidally north of San Diego, is likely an adaptation for avoidance of visual predators. Garibaldi *Hypsypops rubicundus* (Girard, 1854), which are known to prey during the day on sessile animals, including bryozoans and nudibranchs (Clarke 1970), are abundant in the clear, shallow waters around La Jolla (personal observations). Diel variation in the species richness, composition and abundance of nudibranchs out in the open, with higher richness at night, has been observed in tropical and warm-temperate regions in or adjacent to the Indo-Pacific (Johnson 1989; Chang et al. 2013; Larkin et al. 2018), which is known for its high diversity of shore and reef fish (Lieske and Myers 2002). Since we usually started our spring and summer sampling at Tar Pits shortly after dawn (and sampled infrequently in summer), our results on 22 August 2017 suggest we may have under-sampled *J. anulatus* and perhaps not accurately documented its population dynamics at Tar Pits. Future studies of nudibranchs at this site should include more sampling at night, especially in summer.

Owing to the broad range and diversity of prey consumed by heterobranchs (e.g., Thompson 1976; McDonald and Nybakken 1997), the 52 species of heterobranchs we observed at Tar Pits Reef indicate a rich underlying biodiversity of sessile biota, especially for such a small site. Macroalgae have been relatively well documented by MARINE at Tar Pits (e.g., https://marine.ucsc.edu/sitepages/carpinteria_species.pdf), but in order to adequately document the biodiversity of sessile encrusting fauna comprising the prey of Nudipleura at this site, future surveys will require employing field biologists and taxonomists experienced collecting and identifying Porifera, Hydrozoa, Anthozoa, Kamptozoa, Bryozoa, and Ascidiaceae.

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Appendix

Nudibranchs collected by JG at Tar Pits Reef, Carpinteria and deposited in the Invertebrate Zoology Collection at the California Academy of Sciences (CASIZ) in San Francisco, California. Species are listed by their bionomial names used in the online CASIZ database, along with (1) updated names (as accepted by the World Register of Marine Sciences [WoRMS] as of 18 February 2021), (2) CASIZ catalog numbers, and (3) date collected. All specimens were collected in the low rocky intertidal, with the site variously labelled in the CASIZ database for different specimens as Carpinteria State Beach, Carpinteria Reef, Carpinteria, Carpinteria: Tarpits, but all were from Tar Pits Reef, the site name (and spelling) more recently settled on by the senior author.

Species	Updated name	CASIZ Catalog number	Date collected
<i>Flabellina goddardi</i>	<i>Pacifia goddardi</i>	182590	8-May-08
<i>Flabellina goddardi</i>	<i>Pacifia goddardi</i>	186806	20-May-11
<i>Flabellina goddardi</i>	<i>Pacifia goddardi</i>	186807	20-May-11
<i>Flabellina goddardi</i>	<i>Pacifia goddardi</i>	195985	20-Jun-12
<i>Acanthodoris rhodoceras</i>	(no change)	186800	21-May-11
<i>Hancockia californica</i>	(no change)	186801	8-May-08
<i>Janolus anulatus</i>	(no change)	189420	9-May-12
<i>Flabellina</i>	<i>Orienthella cooperi</i> ¹	195988	11-Mar-13
<i>Flabellina iodinea</i>	<i>Flabellinopsis iodinea</i>	195995	20-May-11
<i>Flabellina iodinea</i>	<i>Flabellinopsis iodinea</i>	195996	20-May-11
<i>Flabellina iodinea</i>	<i>Flabellinopsis iodinea</i>	195997	11-May-12
<i>Flabellina iodinea</i>	<i>Flabellinopsis iodinea</i>	195999	20-May-12
<i>Flabellina trilineata</i>	<i>Orienthella trilineata</i>	196003	11-May-13

¹ Identified by JG 18 Feb 2021 based on original notes at collection.

Inventory of the Carabid Beetle Fauna of the Gaoligong Mountains, Western Yunnan Province, China: Species of the Tribe Omophronini (Coleoptera: Carabidae), with a Key and Review for All Species Recorded from China

David H. Kavanaugh ¹, Roberta L. Brett ¹, Hongbin Liang ²

¹ Department of Entomology, California Academy of Sciences, 55 Music Concourse Drive, Golden Gate Park, San Francisco, CA 94118, USA. ² Key Laboratory of Zoological Systematics,

Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China

Corresponding author: David H. Kavanaugh (dkavanaugh@calacademy.org)

Our study of 343 specimens of omophronine carabid beetles collected during a ten-year biodiversity inventory project in the Gaoligong Shan region of western Yunnan Province, China, recognized three different species of genus *Omophron* Latreille, all previously described. We present a key for identification of adults of these species, as well as nomenclatural data, diagnoses, illustrations of dorsal habitus and male and female genitalia and information about geographical, altitudinal and habitat distributions within the study area and overall geographical distribution for each species. Distributions of the species within the study area are compared and broader geographical range patterns are characterized. We also present a review of the nine *Omophron* species now known to occur in China, provide a new key for identification of the Chinese species and summarize the known geographical ranges of each of these species. Two new synonymies are proposed (*O. parvum* Tian & Deuve, 2000 = *O. gemmeum* Andrewes, 1921; and *O. yunnanense* Tian & Deuve, 2000 = *O. stictum* Andrewes, 1933) and a lectotype is designated for *O. stictum* Andrewes.

Keywords: Coleoptera, Carabidae, Omophronini, *Omophron*, China, Yunnan, Gaoligong Shan, new synonymies, distribution, biodiversity hotspot

The Gaoligong Shan (Gaoligong Mountains) of extreme western Yunnan Province, China (Fig. 1) represents the southeasternmost extension of the Transhimalaya (Akeziz et al. 2008). The range extends for more than 600 km north to south and, in the central part of the range, its crest forms the border between China and Myanmar. It also separates and forms parts of the watersheds of two of Southeast Asia's major rivers, the Irrawaddy and the Salween (known in China as the Nujiang). Elevations within the region range from a low of about 650 m in the south to more than 5000 m in the north. Chaplin (2006) reviewed the physical geography of the region. Because of its geographic isolation and rugged topography, much of this area has remained less disturbed than most other parts of China. Previous biological exploration of the area over the past 150 years has revealed exceptionally high species richness, based almost exclusively on records for vertebrates (e.g., Stattersfield et al. 1998) and vascular plants (Li et al. 2000). Because of these traits, two large nature reserves have been established in the area, and the region has been included in the Three Parallel Rivers of Yunnan World Heritage Site (UNESCO 2003).

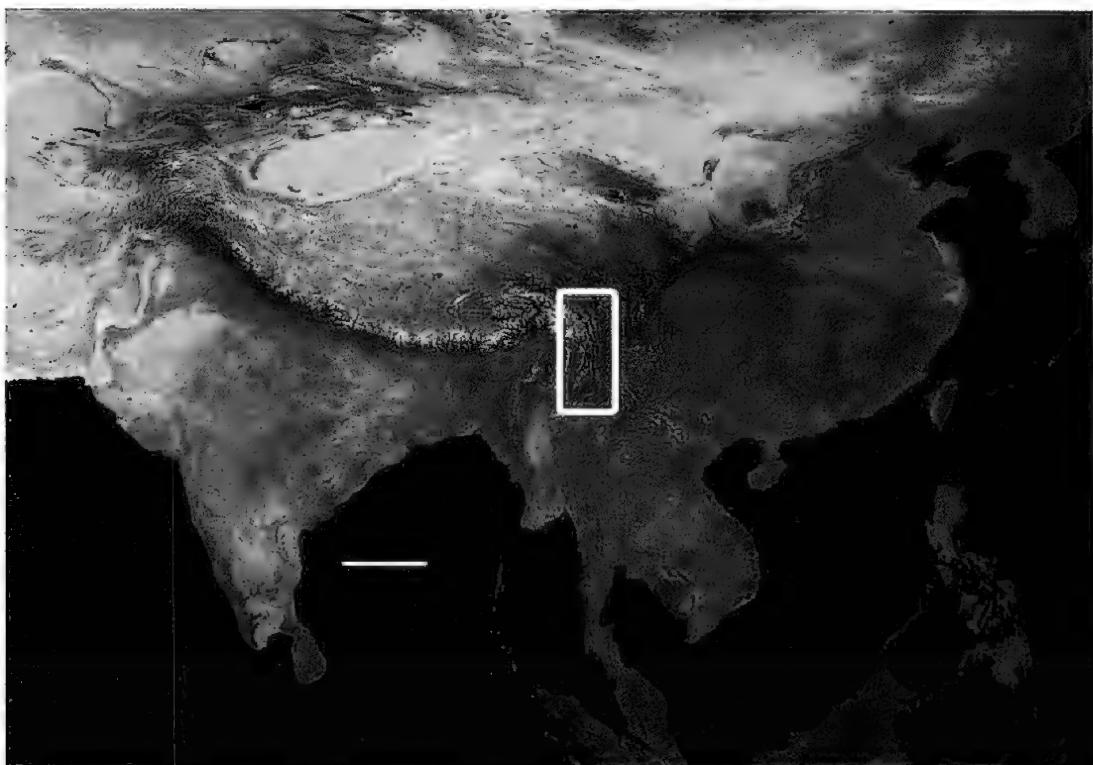


FIGURE 1. Map of Asia with study region outlined; scale line = m 500 km. Modified from Wikimedia Commons, World Atlas of the World, at URL: <http://upload.wikimedia.org/wikipedia/commons/8/8f/Whole_world_-_land_and_oceans_12000.jpg>. Scale line = 500 km.

In late 1997, the California Academy of Sciences was invited to participate in a joint project with the Kunming Institutes of Botany and Zoology of the Chinese Academy of Sciences to conduct a biodiversity inventory of the Gaoligong Mountains. Scientists from several additional institutions, including the Institute of Zoology, Beijing, and Royal Botanical Garden (Edinburgh) joined in the collaboration. Principal target groups for the inventory included bryophytes and vascular plants, all vertebrate groups, arachnids, myriapods and insects, especially the Neuropteroidea, Mecoptera, and Coleoptera (the Carabidae in particular). Multidisciplinary and multi-institutional teams carried out biotic sampling through more than 25 separate expeditions during the period 1998 to 2007. Numerous reports on the project have been published to date, including partial results for bryophytes, higher plants, birds, amphibians, fishes, spiders and carabid beetles (see Deuve et al. 2016 for pertinent references).

This report, on the tribe *Omophronini*, the so-called “Round Sand Beetles”, represents the third of an intended series of treatments on the carabid beetle fauna of the Gaoligong Shan region, each dealing with one or more tribes or genera represented in the fauna. The first two reports (Kavanaugh et al. 2014, Deuve et al. 2016) described the zabrine (Carabidae: Zabroni) and trechine (Carabidae: Trechini) faunas of the region, respectively. Subsequent reports will appear as taxonomic work on each group is completed and not in any particular taxonomic or phylogenetic order.

Omophronini is a modestly diverse taxon, currently including nearly 70 described species (Lorenz 2005; Valainis 2010a, 2010b, 2011 and 2013), all in a single genus, *Omophron* Latreille, 1802. Two subgenera have been recognized: *Phrator* Semenov, 1922a, which includes nine species (Valainis 2016), and the nominate subgenus, which includes the remaining species. *Phrator* is

mainly Afrotropical in distribution, with a single species, *O. variegatum* Olivier, occurring in southern Europe. Roughly one quarter of the species of subgenus *Omophron* are each represented in the Afrotropical and Nearctic plus northernmost Neotropical Regions, respectively, and the remaining half occurs in the combined Palearctic and Oriental Regions. In this last region, highest species diversity is found along the southern base of the Himalaya, especially in eastern India, where at least 13 species occur. The genus does not occur in Australia or South America.

As their common name implies, these beetles occur almost exclusively on sandy substrate, as both adults and larvae. They prefer the open sandy beaches of small to large streams, the sandy shores of lake or ponds, and even sandy ocean shores in areas where freshwater streams or seeps are nearby. At night, they are active on the sand surface in wet, damp, or even dry areas, where they hunt for their small invertebrate prey. In the daytime, they hide by burrowing under stones on the sand surface or into the sand itself. They are easily flushed from these hiding places by splashing water up onto the sand in which they are hiding. Both adults and larvae are most easily collected by searching the beaches at night using a headlamp or by using the splashing technique in daytime.

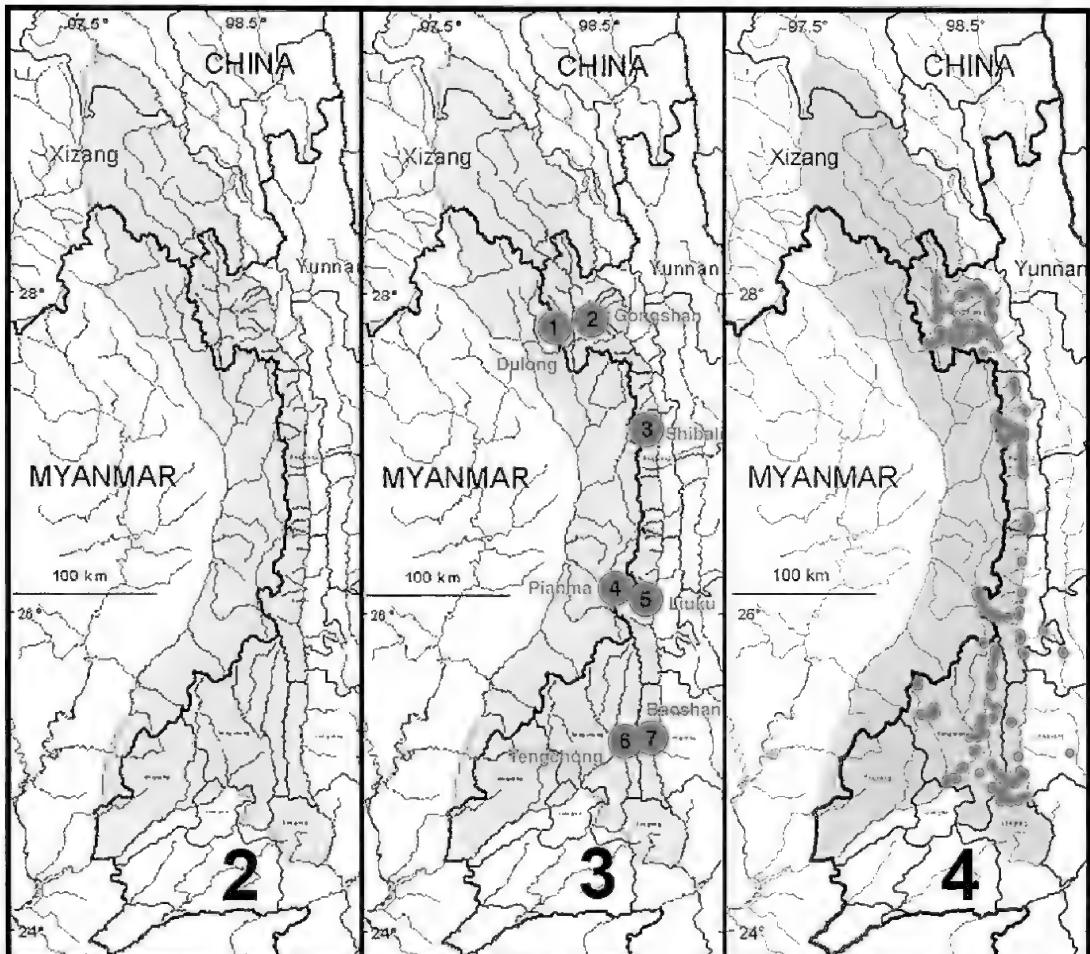
As is the case with most other terrestrial arthropod groups, the *Omophron* fauna of the study area has not been documented previously. Most of our current knowledge of the southeast Asian regional fauna for the genus is from the works of Andrewes (1929), Bänninger (1918, 1921), Chaudoir (1868), and Tian & Deuve (2000), with significant additional contributions from Andrewes (1919, 1921a, 1921b, 1933), Chaudoir (1850, 1852), Darlington (1967), Gestro (1888, 1892), Gistel (1848), Pasco (1860), Valainis (2013), Wrase (2002) and Wiedemann (1823). Tian & Deuve (2000) provided a first review of the *Omophron* fauna of China, Andrewes (1929) summarized the fauna for British India (including at least parts of Nepal, Bangladesh, Myanmar, Laos, and Vietnam), and Valainis (2010b) reviewed the fauna for the Palearctic Region. Because of its particular geographical location, the Gaoligong Shan region has been largely peripheral to each of these other studies.

Based on our study of the material collected for the project and additional specimens from the region housed in other collections, we recognize a total of three *Omophron* species found to occur in the study area. We present here a key for identification of adults of these species, as well as nomenclatural data, diagnoses, illustrations of dorsal habitus and male and female genitalia, and information about geographical and habitat distributions within the study area and overall geographical distribution for each species. We also discuss geographical distributions of the species with respect to different parts of the study area (see below about “core areas”) and to each other, as well as the broader geographical range patterns and the altitudinal ranges of the species.

In order to reach our taxonomic conclusions about the identities of the Gaoligong Shan species, we reviewed material representing most of the known Eurasian species, including type material wherever possible. Having made the necessary critical comparisons, we take advantage here of the opportunity to present a review of the *Omophron* fauna of China, with a key for identification of adults of all the species now known to occur in China. We propose two new synonymies among these species, one of which involves a species represented in the study area.

MATERIALS AND METHODS

The natural physiographic limits of the study area for the project are as shown in Fig. 2 and include areas in eastern Myanmar and southern Xizang (Tibet); but we had permission to survey only those parts in Yunnan Province. Specialists for all taxonomic groups concentrated their efforts on seven core areas within the project region (Fig. 3), selected to facilitate comparisons of possible north to south and east to west spatial differences within the regional biota, as well as recognition of areas of local endemism. Other areas were sampled as time and opportunity permitted. The



FIGURES 2-4. Fig. 2. Map showing natural extent of study area, colored in green (however, sampling was permitted only in those portions in Yunnan Province. Fig. 3. Map showing location of core sampling areas. Fig. 4. Map showing locations of all entomological sampling sites.

entomological team made a total of 13 expeditions to the Gaoligong region. Our sampling sites within the region are shown in Fig. 4. Habitats included in the study area range from subtropical lowland rainforest to the margin of glaciers and snowfields. In all, more than 35,000 carabid specimens were collected during the project by using a variety of collecting methods, including hand collecting both day and night, beating vegetation, sifting litter with subsequent extraction by hand or by mini-Winkler units, and Malaise flight traps and pitfall traps. All specimens were sorted to morphospecies (i.e., presumptive species units based on features of external structure and male and female genitalic traits) and detailed systematic studies of taxonomic groups are ongoing.

This study is based on the examination of 343 specimens of *Omophron* species from the Gaoligong Shan region and more than 150 additional specimens from other regions, representing other *Omophron* species known to occur in Asia. Specimens acquired during our fieldwork have been divided among and are deposited in collections of our home institutions. Codens used throughout this report for collections in which specimens, including primary types, are deposited are as follows:

BMNH	British Museum (Natural History), London, United Kingdom
CAS	California Academy of Sciences, San Francisco, U.S.A.
DWW	David W. Wrane, Gusow-Platkow, Germany (working collection, part of Zoologische Staatssammlung München)
IOZ	National Zoological Museum of China, Institute of Zoology, Beijing, China
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
MNHN	Muséum National d'Histoire Naturelle, Paris, France
SCAU	South China Agricultural University, Guangzhou, China
ZIN	Zoological Institute Academy of Sciences, St. Petersburg, Russia
ZMUC	Zoological Museum, University of Copenhagen, Denmark
ZMUS	Zoological Museum, University of Zürich, Switzerland

Measurements. The following measurements were recorded: body length (BL), measured longitudinally from the anterior margin of the clypeus to the apex of the longer elytron; and maximum body width (EW), measured transversely across the widest part of the elytra. Measurements were taken with the aid of a calibrated ocular micrometer scale on a Wild M5 stereoscopic dissecting microscope.

Dissections of male and female genitalia were prepared from specimens relaxed in hot (near boiling) soapy water by severing the membranes between the genital capsule and tergite VII and sternite VII and extracting the capsule intact. The dissections were then cleared in warm 10% KOH and further dissected to separate the sclerotized parts enough to visualize structures to be compared. Following dissection, preparations of female genitalic structures were stained with Chlorosol Black E. Terms used for structures of the female reproductive tract follow those used by Liebherr & Will (1998).

Illustrations. Digital images of dorsal habitus were taken using a Canon EOS 6D Mark II DSLR camera with a 65mm 2.8-5X macro lens. Multiple images at different focal planes were taken using a StackShot Macro Rail Package and merged using Helicon Focus software. Multiple digital images of tarsi and male and female reproductive structures were taken and merged using an Automontage imaging system from Synchroscopy with a JVC KY-F-75U digital camera and a Leica M420 dissecting microscope. Final images were cleaned of extraneous items in view and adjusted for brightness and contrast using Adobe Photoshop CS6. Consequently, these images may have artefacts of the merging algorithm and subsequent image processing. A "CASENT" number associated with an image, as noted in figure captions, is a unique identifier that refers to the particular specimen photographed and its CAS database record. Distribution maps for each species in the study area were generated from geographical coordinate data maintained in a Biota Version 3.0 database (Colwell 2012) using the ArcMap program in ArcGIS for Desktop Version 10.2 software from Esri.

Comment. The form and extent of maculation patterns on the head, pronotum and elytra of *Omophron* have been used extensively in the past and are used in this work to help distinguish members of different *Omophron* species. However, interpretation of the extent of the maculae, especially on the pronotum but also on the elytra and head, is complicated by the tendency in many specimens with a pale background coloration to exhibit dark brown discoloration that extends beyond the maculae themselves and thereby exaggerates their extent or changes their form. This discoloration appears to be mainly in areas where internal tissues (e.g., muscle) have been discolored and/or shrunk away from the body wall in dried specimens. For our purposes, we define the shape and extent of all maculae as the areas that exhibit at least faint metallic reflection or distinctly dark (black or piceous) coloration and do not include the areas of brown discoloration alone.

TAXONOMY

Adult specimens of *Omophron* species represented in the Gaoligong Shan region can be distinguished using the following key.

Key for identification of adults of *Omophron* species of the Gaoligong Shan region

- 1 Size large, body length (BL) males or females greater than 5.5 mm; silhouette (dorsal aspect) distinctly angulate at junction of pronotum and elytra, forebody slightly but clearly narrower than elytra; pale area on frons thickly V-shaped; antennomere 1 with two apical setae, antennomeres 3 and 4 with several setae laterally in addition to apical setal whirl; elytra each with 15 striae, all distinct and equally impressed throughout, elytral intervals all slightly convex and with a midline row of very fine, shallow punctures, elytral maculation pattern as in Fig. 5A. *O. pseudotestudo* Tian & Deuve
- Size small, body length (BL) males or females less than 5.0 mm; silhouette (dorsal aspect) short, oval, forebody as wide as elytra or nearly so, junction of pronotum and elytra not at all or only slightly angulate; pale area on frons restricted to a small, pale, medial triangular area or absent; antennomere 1 with a single apical seta, antennomeres 3 and 4 without lateral setae (i.e., with apical whirl of setae only); elytra each with 15, 14 or 13 striae, variously but all more shallowly impressed and more or less effaced at least apically, elytral intervals 1 to 8 flat, intervals 9 to 15 flat or slightly convex, all intervals without midline row of punctures, maculation pattern as in Figs. 9A-D, 12A-B 2
- 2 Male protarsomere 1 greatly enlarged (Fig. 8C), distinctly wider than apex of mesotibia and longer than tarsomeres 2 to 4 combined; male mesotarsomere 1 also enlarged, as wide as mesotibial apex; elytra each with 15 striae near base, but striae 14 extended apically only to basal one-third; dorsal dark areas dark brown, without metallic reflection, elytral silhouette slightly elongate, widest at basal one-fifth, elytral maculation pattern as in Fig. 12A. *O. chelys* Andrewes
- Male protarsomere 1 only slightly enlarged (Fig. 8B), narrower than apex of tibia and about as long as tarsomeres 2 to 4 combined; male mesotarsomere 1 only slightly enlarged, narrower than mesotibial apex; elytra each with 13 striae (striae 1 to 12 and 15) at basal one-third, striae 13 and 14 each present only as one to four punctures in basal one-fifth; dorsal dark areas with bright green or blue-green metallic reflection, elytral silhouette slightly shorter and more rounded, widest at basal one-fourth, elytral maculation pattern as in Figs. 9A-D *O. gemmeum* Andrewes

1. *Omophron pseudotestudo* Tian & Deuve, 2000

Figures 5A-B, 6A-B,D-E, 7A-B,D, 8A, 13A, 14A, 15

Omophron pseudotestudo Tian and Deuve, 2000:67. Holotype [not seen], a male, deposited in SCAU; two paratypes, one male and one paratype female, also from SCAU [both examined]. Type locality: China, Yunnan, Xishuangbanna, "Jinghong".

Notes on nomenclature and types. We compared specimens from the study area with type specimens of both *O. testudo* Andrewes, 1919 and *O. pseudotestudo*. Members of these two species are similar in most characters of external form and structure. All have antennomere 1 with two apical setae and antennomeres 3 and 4 with several setae laterally in addition to the apical setal whirl, the elytral intervals with a row of fine punctulae along the midline and abdominal ventrite 5 setose. They share head, pronotal and elytral maculation patterns that are similar in general form, with variation in the extent of the dark bands of elytra maculation pattern overlapping in the two

species. We initially suspected that these two samples were conspecific and their names should be considered synonymous. However, we observed that two (the male “type” and one female) of the three specimens of the type series of *O. testudo* that we received on loan from BMNH were slightly larger (BL = 7.5 mm) and had the pronotum (Fig. 5C) broader basally than the third specimen (a female). The two were from the type locality (see below) in Laos, whereas the third specimen was from a locality in Vietnam and had the same pronotal shape as paratype specimens of *O. pseudotestudo* (Fig. 5B) and specimens from the study area (Fig. 5A) and was within the size range of these beetles as well (BL = 7.0 mm). Genitalic dissections of all three type specimens proved highly informative. The median lobe of the aedeagus of the male is more expanded subapically and more narrowed apically in dorsal aspect (Fig. 6C) and more slender and less arcuate in left lateral aspect (Fig. 6F) than those of *O. pseudotestudo* (Fig. 6B) males and males from the study area (Fig. 6A and 6D), respectively. The female specimen from the type locality has a helminthoid sclerite (Fig. 7C) that extends further posteriorly in the bursa copulatrix and is distinctly recurved dorsally and markedly expanded as a curved, cup-like plate at its terminus in the dorsal lobe of the bursa. The helminthoid sclerite of the female specimen from Vietnam (Fig. 7D), the female paratype of *O. pseudotestudo* (Fig. 7B), and females from the study area (Fig. 7A) does not extend as far posteriorly in the bursa copulatrix, is not recurved dorsally, and is corkscrew-shaped in the dorsal lobe of the bursa and only slightly expanded at its terminus. In addition, the insertion point for the spermathecal duct (Liebherr & Will 1998) on the dorsal lobe of the bursa is on the posterior face of the lobe in the female from Laos but on the anterior face, at the end of the helminthoid sclerite, in the other specimens. Consequently, we conclude that *O. testudo* and *O. pseudotestudo* are distinct species and that the female of *O. testudo* from Vietnam (see below) is instead a member of *O. pseudotestudo*. Because of the mixed identity of specimens in the type series of *O. testudo*, its type locality should be restricted to Laos, Houaphan Province, Ko Kieng area, where the holotype (“type”) was collected.

Andrewes (1919: 294) indicated that he had seen five specimens of his new species from the type locality (as restricted above) plus the specimen from “Tranninh” and another from “Annam: Keng Trap”; so there are four specimens which we have not examined that also should be considered as part of the type series of *O. testudo*. One of these is apparently the specimen (in ZMUZ) from “Keng Trap”, labeled as a “cotype” of *O. testudo*, a photograph of which can be found on the *Carabidae of the World* website at <<http://carabidae.org/taxa/testudo-andrewes-1919>>. Pronotal shape of this specimen suggests that it may also represent *O. pseudotestudo* rather than *O. testudo*.

Diagnosis. Adults of this species (Fig. 5A) can be distinguished from those of other species in the region by the following combination of character states: size large, BL of males 5.8 to 6.8 mm and of females 6.2 to 7.1 mm, EW of males 4.1 to 5.0 mm and of females 4.3 to 5.1 mm; silhouette (dorsal aspect) distinctly angulate at junction of pronotum and elytra, forebody slightly but clearly narrower than elytra; dorsal darkened areas with dark green or blue-green metallic reflection; pale area on frons thickly V-shaped; antennomere 1 with two apical setae, antennomeres 3 and 4 with several setae laterally in addition to apical setal whirl; elytra each with 15 striae, all distinct and equally impressed throughout, elytral intervals all slightly convex and with a midline row of very fine, shallow punctures, elytral maculation pattern as in Fig. 5A; male protarsomere 1 only slightly enlarged (Fig. 8A), narrower than apex of tibia and about as long as tarsomeres 2 to 4 combined; abdominal ventrite 5 asetose; median lobe of male genitalia as in Fig. 6A-B; helminthoid sclerite of spermathecal duct of female reproductive tract as in Fig. 7A-B,D.

The elytral maculation pattern is similar in form but varied in the extent of the dark areas among *O. pseudotestudo* specimens. The paratype male of *O. pseudotestudo* (Fig. 5B) has the most extensive dark elytral maculation we have seen, whereas the holotype male illustrated by Tian &

Deuve (2000) and paratype female we examined have elytral maculation more similar to specimens from the study area (Fig. 5A).

Geographical distribution within the Gaoligong Shan. Fig. 13A. We examined a total of 285 specimens (164 males and 121 females) from the following localities: **Tengchong County:** Mangbang Township (Longchuan Jiang at Longwenqiao in Shangying village, N25.02396°/E98.67675°, 1285 m, 5 June 2006, D.H. Kavanaugh, R.L. Brett, H.B. Liang & D.Z. Dong collectors [three males; CAS, IOZ]); Qushi Township (Longchuan Jiang at Longkou village, N25.28167°/E98.59167°, 1500 m, 22 October 2003, H.B. Liang & X.C. Shi collectors [one female; IOZ], N25.28175°/E98.59246°, 1500 m, 6 June 2006, D.H. Kavanaugh & R.L. Brett collectors [six males and four females; CAS, IOZ]), (Longchuan Jiang at Xiaojiangqiao, N25.23944°/E98.61667°, 1445 m, 21 October 2003, H.B. Liang & X.C. Shi collectors [four males and one female; CAS, IOZ], N25.23939°/E98.62723°, 1440 m, 24 May 2006, D.H. Kavanaugh, R.L. Brett, H.B. Liang & D.Z. Dong collectors [34 males and 32 females; CAS, IOZ]), (Longchuan Jiang at Yonganqiao, N25.32502°/E98.60959°, 1470 m, 24 May 2006, D.H. Kavanaugh, R.L. Brett & H.B. Liang collectors [three males and seven females; CAS, IOZ]); Wuhe Township (Longchuan Jiang at Longjiangqiao, N24.89889°/E98.66667°, 1215 m, 28 October 2003, H.B. Liang & X.C. Shi collectors [18 males and 13 females; CAS, IOZ], 30 October 2003, H.B. Liang & H.B. Shi collectors [73 males and 47 females; CAS, IOZ]), (Longchuan Jiang just below bridge at Menglian village, N24.89176°/E98.67551°, 1230 m, 3 June 2006, D.H. Kavanaugh, R.L. Brett, H.B. Liang & D.Z. Dong collectors [21 males and 10 females; CAS, IOZ]), (Longchuan Jiang, west bank at Tongjiazhuang village, N24.89284°/E98.67439°, 1210 m, 24 May 2005, H.B. Liang collector [one male and five females; CAS, IOZ], N24.89499°/E98.67510°, 1205 m, 24 May 2005, D.H. Kavanaugh, C.E. Griswold & D.Z. Dong collectors [one male and one female; CAS]).

Members of this species were collected only in the southwestern part of the study area (Core Area 6), despite sampling in similar habitats throughout the Gaoligong Shan region. We suggest that this apparent restriction is real and not based simply on inadequate sampling elsewhere in the study area.

Habitat distribution. Within the study area, members of this species have been found only on open sandy shores of the Longchuan Jiang (Fig. 14A), a medium-sized river, where they remain buried in the sand during daylight hours and are active on the sand surface in moist areas at night. A few specimens have also been collected during the day from under small stones and drift debris in the same habitat. In all but one locality in which they have been found, they co-occur with members of *O. gemmeum*. Within the Gaoligong Shan region, this species occurs at relatively low elevations, with our records documenting its occurrence in the 1205 to 1500 m range.

Overall geographical distribution. Fig. 15. This species has been recorded from China (Yunnan), India (Assam, Sikkim) and Vietnam. Its occurrence in the study area is near the midpoint of both its known east/west and north/south geographical ranges.

Geographical relationships with other *Omophron* species. Within the study area, members of this species are found together with those of *O. gemmeum* (see below) on the same sandy beaches. These two species are not closely related and, in fact, are members of different species groups. Outside the study area, their ranges overlap broadly, from northern Vietnam in the east to Sikkim in the west. The range of *O. pseudotestudo* also overlaps with that of *Omophron porosum* Chaudoir, 1868 in western Assam, with *Omophron oberthueri* Gestro, 1892 and *O. chelys* in Sikkim, with *Omophron stictum* Andrewes, 1933 in southcentral Yunnan and with *Omophron saigonense* Chaudoir, 1868 in Vietnam.

2. *Omophron gemmeum* Andrewes, 1921

Figures 8B, 9A-D, 10A-B,D-E, 11A-B, 13B, 14A, 15

Omophron gemma Andrewes, 1921a:406. Holotype [examined], a male, deposited in BMNH. Type locality: India, "Kumaon" [Uttarakhand], western Almora District.

Omophron gemmeus Andrewes 1921b:190 [replacement name for *O. gemma* Andrewes, a junior homonym of *Omophron gemma* Casey, 1897:304]; Andrewes 1929:157.

Omophron parvum Tian and Deuve, 2000:67. Holotype [examined], a female, deposited in SCAU; one female paratype, also in SCAU [not seen]. Type locality: China, Guangxi Zhuang Autonomous Region, Xixiangtang (western suburb of Nanning). **NEW SYNONYMY.**

Notes on nomenclature and types. We compared specimens from the study area with the types of both *O. gemmeum* and *O. parvum*. All are similar in size, body form, surface punctuation and overall pronotal and elytral maculation pattern (Figs. 9A-D). Males of *O. gemmeum* and those from the study area have a similar form of the median lobe and internal sac of their genitalia (Figs. 10A-B). Females of *O. gemmeum*, the holotype of *O. parvum* (Fig. 11B), and females from the study area (Fig. 11A) have a very similar helminthoid sclerite of the bursa copulatrix. Although there is some variation in the extent of elytral maculation throughout the geographical range of this species, specimens from the western part of its range, represented by the holotype of *O. gemmeum* (Fig. 9A), tend to have the most laterally extensive dark elytral pattern; those from the eastern part of the range, represented the holotype of *O. parvum* (Fig. 9D), have the most restricted dark pattern. Specimens from the study area, near the middle of the range of the species, are also intermediate in the form of their dark elytral pattern, with examples (Figs. 9C,D) approaching the more extreme western and eastern forms. Based on these observations, we conclude that all of these specimens represent a single species, which is why we here propose synonymy between *O. gemmeum* and *O. parvum*, with the former having priority.

Diagnosis. Adults of this species (Fig. 9A-D) can be distinguished from those of other species in the region by the following combination of character states: size small, BL of both males and females 3.7 to 4.3 mm, EW of both males and females 2.5 to 3.1 mm; silhouette (dorsal aspect) short, oval, forebody as wide as elytra or nearly so, junction of pronotum and elytra not at all or only slightly angulate; dorsal darkened areas with bright green or blue-green metallic reflection; pale area on frons restricted to a small, pale, medial triangular area or absent; antennomere 1 with a single apical seta, antennomeres 3 and 4 without lateral setae (i.e., with apical whirl of setae only); elytra each with 13 striae (striae 1 to 12 and 15) at basal one-third, striae 13 and 14 each present only as one to four punctures in basal one-fifth, elytral intervals 1 to 8 flat, intervals 9 to 15 flat or slightly convex, all intervals without midline row of punctures, maculation pattern as in Figs. 9A-D; male protarsomere 1 only slightly enlarged (Fig. 8B), narrower than apex of tibia and about as long as tarsomeres 2 to 4 combined; male mesotarsomere 1 only slightly enlarged, narrower than mesotibial apex; median lobe of male genitalia as in Figs. 10A-B; helminthoid sclerite of spermathecal duct of female reproductive tract as in Figs. 11A-B.

Adults of *O. gemmeum* are most similar to those of *Omophron brettinghamae* Pascoe. The known geographical ranges of these two species overlap in the region along the southern edge of the Himalaya, from Uttarakhand in the west to Bangladesh in the east; however, we have not yet seen specimens of both species from the same locality within that area of overlap. The two species have been confused, one with the other, in identifications found in several collections (personal communication, David Wrase). Nonetheless, subtle differences in both external and internal features distinguish their members. There is a subtle difference in overall body silhouette in dorsal view, with *O. brettinghamae* adults (Fig. 9E) slightly shorter and more nearly round in form than *O. gemmeum* adults (Figs. 9A-D). Additional external features pointed out to us by David Wrase

include the following: pronotum more coarsely and even punctate, particularly right and left of the midline, in *O. gemmeum* than in *O. brettinghamae*; basal band of the elytral maculation pattern narrowly extended laterally to the humerus or nearly so in *O. gemmeum* but not extended to the humeral region in *O. brettinghamae*. We also observed slight but consistent differences in shape of the median lobe and internal sac of the male genitalia. In *O. gemmeum* males, the median lobe (Figs. 10A-B) is broader throughout and very broadly rounded apically in dorsal aspect, whereas it is more slender and narrowly rounded apically in *O. brettinghamae* males (Fig. 10C). In addition, the internal sac is smoothly arcuate or obtusely bent in lateral aspect (Figs. 10D-E) and nearly straight in dorsal aspect (Figs. 10A-B) in *O. gemmeum* males but sigmoid in both aspects in *O. brettinghamae* males (Figs. 10C,F). The helminthoid sclerite in *O. gemmeum* females (Figs. 11A-B) is longer and straighter posteriorly and abruptly bent dorsally and then to the right in the dorsal lobe of the bursa copulatrix, whereas it is shorter, slightly sigmoid posteriorly and gently curved to the right in *O. brettinghamae* females (Fig. 11C).

Geographical distribution within the Gaoligong Shan. Fig. 13B. We examined a total of 55 specimens (31 males and 24 females) from the following localities: **Tengchong County:** Mangbang Township (Longchuan Jiang at Longwenqiao in Shangying village, N25.02396°/E98.67675°, 1285 m, 5 June 2006, D.H. Kavanaugh, R.L. Brett, H.B. Liang & D.Z. Dong collectors [one male; CAS]); Qushi Township (Longchuan Jiang at Longkou village, N25.28167°/E98.59167°, 1500 m, 22 October 2003, H.B. Liang & X.C. Shi collectors [one female; IOZ]), (Longchuan Jiang at Xiaojiangqiao, N5.23944°/E98.61667°, 1445 m, 21 October 2003, H.B. Liang & X.C. Shi collectors [five males and nine females; CAS, IOZ], N25.23939°/E98.62723°, 1440 m, 24 May 2006, D.H. Kavanaugh, R.L. Brett, H.B. Liang & D.Z. Dong collectors [14 males and five females; CAS, IOZ]); Wuhe Township (Longchuan Jiang at Longjiangqiao, N24.89889°/E98.66667°, 1215 m, 28 October 2003, H.B. Liang & X.C. Shi collectors [eight males and eight females; CAS, IOZ], 30 October 2003, H.B. Liang & X.C. Shi collectors [one male; IOZ]), (Longchuan Jiang just below bridge at Menglian village, N25.89176°/E98.67551°, 1230 m, 3 June 2006, D.H. Kavanaugh, R.L. Brett, H.B. Liang & D.Z. Dong collectors [one male and one female; CAS, IOZ]), (Longchuan Jiang at Tongjiazhuang village, N24.89499°/E98.67510°, 1205 m, 24 May 2005, D.H. Kavanaugh, C.E. Griswold & D.Z. Dong collectors [one male; CAS]).

Members of this species were collected only in the southwestern part of the study area (Core Area 6), despite sampling in similar habitats throughout the Gaoligong Shan region, so we suggest that this apparent restriction is real and not based simply on inadequate sampling elsewhere in the study area.

Habitat distribution. Within the study area, members of this species have been found only on open sandy shores of the Longchuan Jiang (Fig. 14A) a medium-sized river, where they remain buried in the sand during daylight hours and are active on the sand surface in moist areas at night. A few specimens have also been collected during the day from under small stones and drift debris in the same habitat. Outside of the study area, they have also been collected on loam and a mix of sand and loam on the upper river banks under wood, stones or in gravel under scattered vegetation (D.W. Wrase, personal communication). Wherever they have been found in the study area, they co-occur with members of *O. pseudotestudo*. Within the Gaoligong Shan region, this species occurs at relatively low elevations, with our records documenting its occurrence in the 1205 to 1500 m range.

Overall geographical distribution. Fig. 15. This species has been recorded from China (Guangxi and Yunnan), India (Uttarakhand, Sikkim and West Bengal) and Vietnam. Its occurrence in the study area is near the midpoint of its known geographical range.

Geographical relationships with other *Omophron* species. Members of this species are

found together with those of *O. pseudotestudo* (see above) on the same sandy beaches. These two species are not closely related and, in fact, are members of different species groups. Outside the study area, their ranges overlap broadly, from Vietnam in the east to Sikkim in the west. The range of *O. gemmeum* also overlaps with that of *Omophron stictum* in southern Yunnan, with *Omophron porosum* in western Assam, with *Omophron oberthueri* in Sikkim, with *Omophron siagonense* Chaudoir in Vietnam and with several additional species in the westernmost part of its range in Uttarakhand, India. Although the overall geographical ranges of *O. gemmeum* and *O. brettinghamae* either overlap or parallel one another in the region just south of the Himalaya extending from Bangladesh to Uttarakhand and Uttar Pradesh, these two closely related species apparently have not been found together.

3. *Omophron chelys* Andrewes, 1921

Figures 8C, 12A-D, 13C, 14B, 15

Omophron chelys Andrewes, 1921a:404. Holotype [examined], a male, deposited in BMNH. Type locality: India, West Bengal, Darjeeling, Gopaldhara, 2620 m.

Notes on nomenclature and types. A second specimen, a female, in BMNH (labeled: “Inde Anglaise Pedong Région de Darjeeling. Chasseurs indigenes 1935”/ “H. E. Andrewes Coll. B. M. 1945–97.”/ “Ex coll. R. Oberthür.”/ ♀ / “Omophron chelys Andrewes [handwritten] [female symbol] H. E. Andrewes det.”) is not a type specimen but was identified as *O. chelys* by Andrewes. However, examination of the female reproductive system through dissection confirms that it is instead a specimen of *O. gemmeum*.

Diagnosis. Adults of this species (Fig. 12A) can be distinguished from those of other species in the region by the following combination of character states: size small, BL of males 4.0 to 4.5 mm and of females 4.4 to 4.5 mm, EW of males 2.9 mm and of females 3.0 to 3.1 mm; silhouette (dorsal aspect) short, oval, widest at basal one-fifth, forebody as wide as elytra or nearly so, junction of pronotum and elytra not at all or only slightly angulate; dorsal darkened areas dark brown, without metallic reflection; pale area on frons restricted to a small, pale, medial triangular area or absent; antennomere 1 with a single apical seta, antennomeres 3 and 4 without lateral setae (i.e., with apical whirl of setae only); elytra each with 15 striae near base, but striae 14 extended apically only to basal one-third, striae distinctly punctate and more shallowly impressed laterally and more or less effaced at least apically, elytral intervals 1 to 8 flat, intervals 9 to 15 flat or slightly convex, all intervals without midline row of punctures, maculation pattern as in Fig. 12A; male protarsomere 1 greatly enlarged (Fig. 8C), distinctly wider than apex of mesotibia and longer than tarsomeres 2 to 4 combined; male mesotarsomere 1 also enlarged, as wide as mesotibial apex; median lobe of male genitalia as in Figs. 12C-D; helminthoid sclerite of spermathecal duct of female reproductive tract as in Fig. 18A.

Geographical distribution within the Gaoligong Shan. Fig. 13C. We examined a total of three specimens (one male and two females) from the following localities: **Gongshan County:** Dulongjiang Township (Bapo, Mulangdang, 1355 m, N27.75256°/E098.34745° 4 November 2004, Stop#LHB-2004-046, H.-B. Liang collector, [one female; IOZ]), (west bank of Dulong Jiang at Elideng village, 1640 m, N28.00287°/E098.32145°, November 2004, Stop#DHK-2004-073, D.H. Kavanaugh, G. Tang & D.-Z. Dong collectors, [one female; CAS]), (Dulong Jiang at Xianjiudang village, 1580 m, N27.94092°/E098.33340°, 4 November 2004, Stop#DHK-2004-074, D.H. Kavanaugh, M.A. Dixon, G. Tang & D.-Z. Dong collectors, [one male; CAS]).

Members of this species were collected only from the northwestern part of the study area (Core Area 1), despite sampling in similar habitats throughout the Gaoligong Shan region. So we

suggest that this apparent restriction is real and not based simply on inadequate sampling elsewhere in the study area.

Habitat distribution. Members of this species have been found only on the open shores of the Dulong Jiang (Fig. 14B), a medium-sized river, in areas with a mix of sand and stones. They remain buried in the sand or under stones during daylight hours and are active on the sand surface in moist areas at night. This species is found at relatively low elevations in the region, with our records documenting its occurrence between 1355 and 1640 m.

Overall geographical distribution. Fig. 15. This species currently is known only from the type locality in Sikkim, India, from Bomi and Medong counties in Xizang (Tibet) and from several localities along the Dulong Jiang, an eastern tributary of the Irrawaddy River, which gathers the western drainage of the northern Gaoligong Shan. To date, it has been recorded only in that portion of the river in westernmost Yunnan Province, China, but we suspect that it may occur further downstream along the Dulong Jiang, at least in adjacent parts of easternmost Myanmar, and probably also in Arunachal Pradesh, India, and Bhutan.

Geographical relationships with other *Omophron* species. No other *Omophron* species is known to occur in that part of the Gaoligong Shan region occupied by *O. chelys*. Outside of the study area, this species is known only from its type locality in the Darjeeling region of West Bengal, India, where its range overlaps that of *O. oberthueri*. Specimens of *O. gemmeum* have been collected together with those of *O. oberthueri* in nearby Sikkim, so it is possible that *O. chelys* and *O. gemmeum* also occur together in this region.

DISCUSSION

The Gaoligong Shan region is at the heart of one of the world's biodiversity hotspots (Myers et al. 2000), as well as near the center of the Asian distribution of genus *Omophron*. Even with the two new synonymies proposed here, the Asian fauna includes 27 *Omophron* species, nearly half of the world's diversity. None of the three species we recorded from the area, based on material from our ten years of sampling plus additional records from collections (see list in Materials and Methods section above), is new to science or endemic to the area. Nonetheless, the composition of the *Omophron* fauna of the area is of interest on several levels.

Broad geographical distribution patterns. The known overall geographical ranges of the three species, superimposed on one another, are graphically approximated in Fig. 15. Among the geographical ranges of these species, two general range patterns are apparent. The first is that shown by *O. chelys*, with a geographical range that includes only the Himalayan region immediately to the west (to northwestern West Bengal) and the northwestern slope of the Gaoligong Shan region. This distribution pattern is similar to that seen among a few species of *Amara* represented in the Gaoligong Shan fauna (Kavanaugh et al. 2014). The second pattern is that shown by *O. pseudotestudo* and *O. gemmeum*. The known geographical ranges of each of these species include the Gaoligong Shan region and areas of varied distance toward both the northwest, along the southern edge of the Himalaya, and the southeast. Of these, the range of *O. gemmeum* extends farther east (to Guangxi Province) and west (at least to Uttarakhand), whereas the known range of *O. pseudotestudo* extends from westernmost Assam to eastcentral Vietnam. The western part of this range pattern is also seen among some *Amara* (Kavanaugh et al. 2014) and trechine species (Deuve et al. 2016), but none of those species share the eastern part of the ranges of the *Omophron* species, which extend southeast to Vietnam or western Quangxi. Instead, the eastern extent of their ranges is farther to the north, either broadly across central and northern Asia or more narrowly along the southern margin of the Tibetan Plateau.

Regional geographical and altitudinal distribution patterns. Within the Gaoligong Shan

study area, all three of the species represented are narrowly restricted, both geographically and altitudinally. This is not surprising given the shared preferences of their members for the open sandy banks of large rivers. Such areas are found only at lower elevations in the study area. All of our records for the region are from the western slope of the Gaoligong Shan, which is part of the Irrawaddy River drainage system. Riverbanks in this part of the study area have pale, yellow-tan sand. In contrast, equivalent riverbanks on the eastern slope of the range, the Nujiang (Salween) River drainage, have finer and grittier greyish sand, which may not suit the physical substrate requirements of these beetles.

As for previous carabid groups examined, we were interested in the occurrence of *Omophron* species in relation to our project-designed Core Areas (Fig. 3) and in the recorded altitudinal ranges for each species. *Omophron chelys* (Fig. 13C) was found to occur only in Core Area 1, at elevations ranging from 1355 to 1640 m, and *Omophron pseudotestudo* and *O. gemmeum* were found only in Core Area 6, at elevations ranging from 1205 to 1500 m.

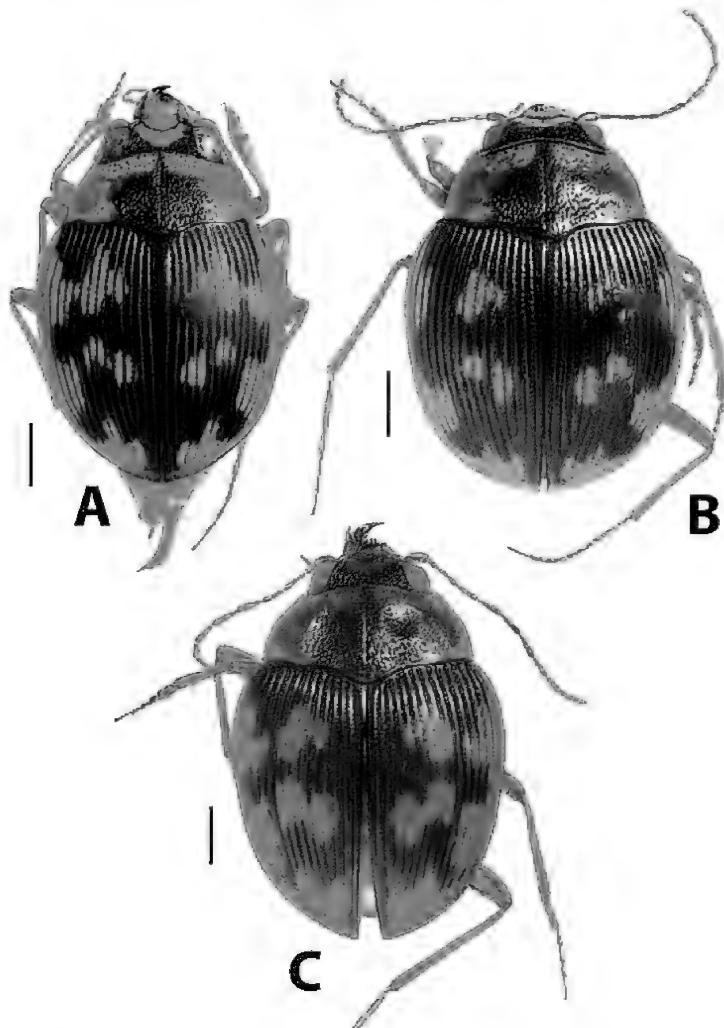


FIGURE 5. Dorsal habitus of *Omophron* species. A. *O. pseudotestudo* Tian & Deuve (CASENT1012671); Longchuan Jiang, Wuhe Township, Tenchong County, Yunnan, China; B. *O. pseudotestudo* (Paratype; Jianhong, Xishuangbanna, Yunnan, China); C. *O. testudo* Andrewes (Holotype; Ko Kieng, Houaphan Province, Laos). Scale line = 1.0 mm.

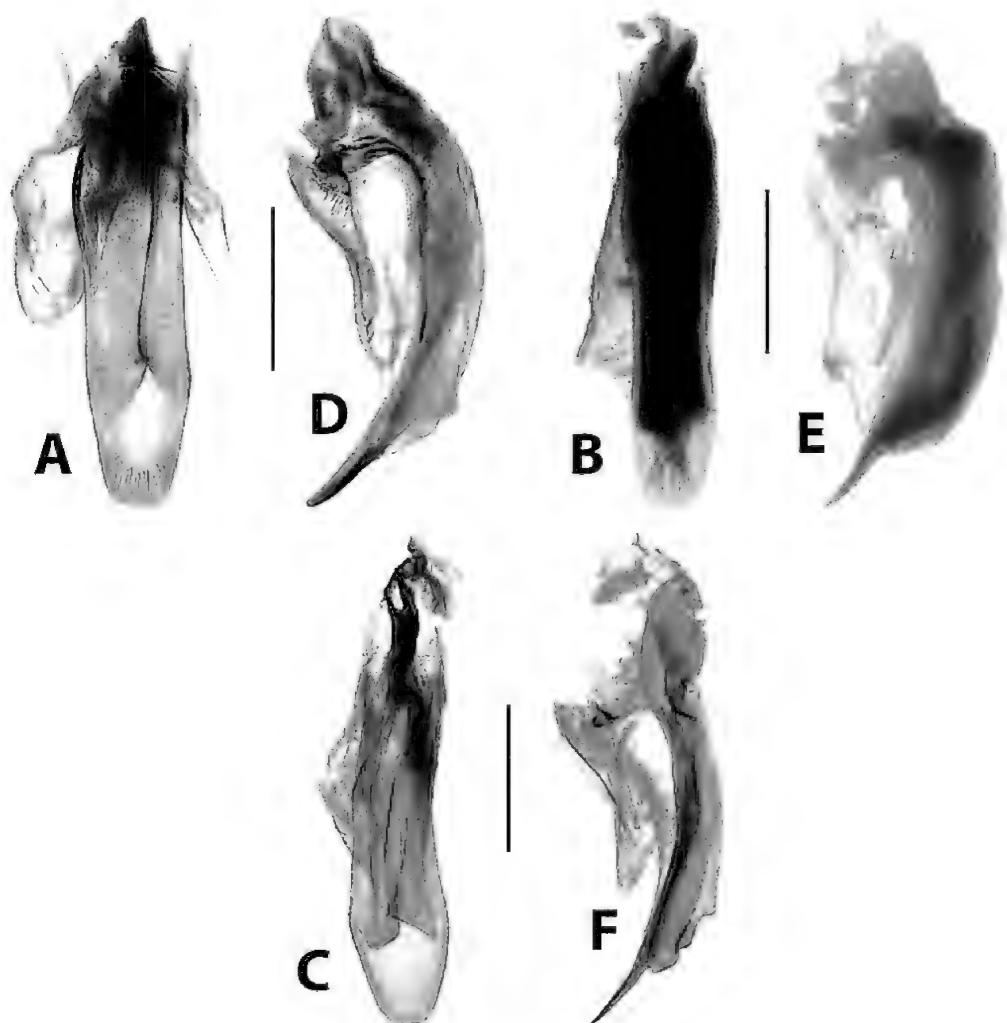


FIGURE 6. Male genitalia of *Omophron* species. A-C, dorsal aspect; D-F, left lateral aspect. A,D, *O. pseudotestudo* Deuve & Tian (CASENT1012726; Longchuan Jiang, Wuhe Township, Tenchong County, Yunnan, China); B,E, *O. pseudotestudo* (Paratype; Jianhong, Xishuangbanna, Yunnan, China); C,F, *O. testudo* Andrewes (Holotype; Ko Kieng, Houaphan Province, Laos). Scale line = 0.5 mm.

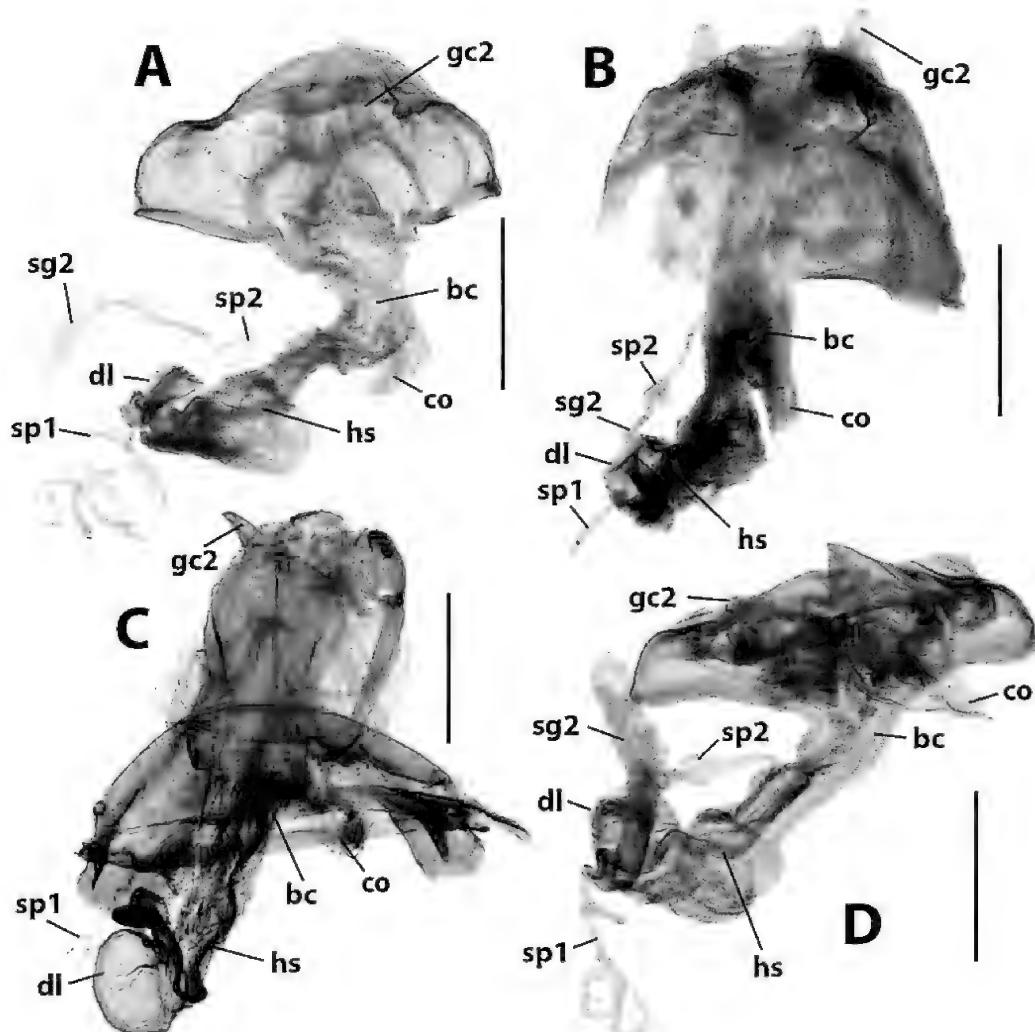


FIGURE 7. Female reproductive tract (dorsal aspect) of *Omophron* species. A. *O. pseudotestudo* (CASENT1012743; Longchuan Jiang, Wuhe Township, Tenchong County, Yunnan, China); B. *O. pseudotestudo* (Paratype; Jianhong, Xishuangbanna, Yunnan, China); C. *O. testudo* ("Cotype"; Ko Kieng, Houaphan Province, Laos); D. *O. pseudotestudo* ("Cotype" of *O. testudo*; "Tonkin, Trannihn" Vietnam); bc = bursa copulatrix; co = common oviduct; dl = dorsal lobe of spermathecal; gc2 = gonocoxite 2; hs = helminthoid sclerite; sg2 = spermathecal gland 2; sp1 = spermatheca 1; sp2 = spermatheca 2 (sensu Liebherr & Will 1998). Scale line = 0.5 mm

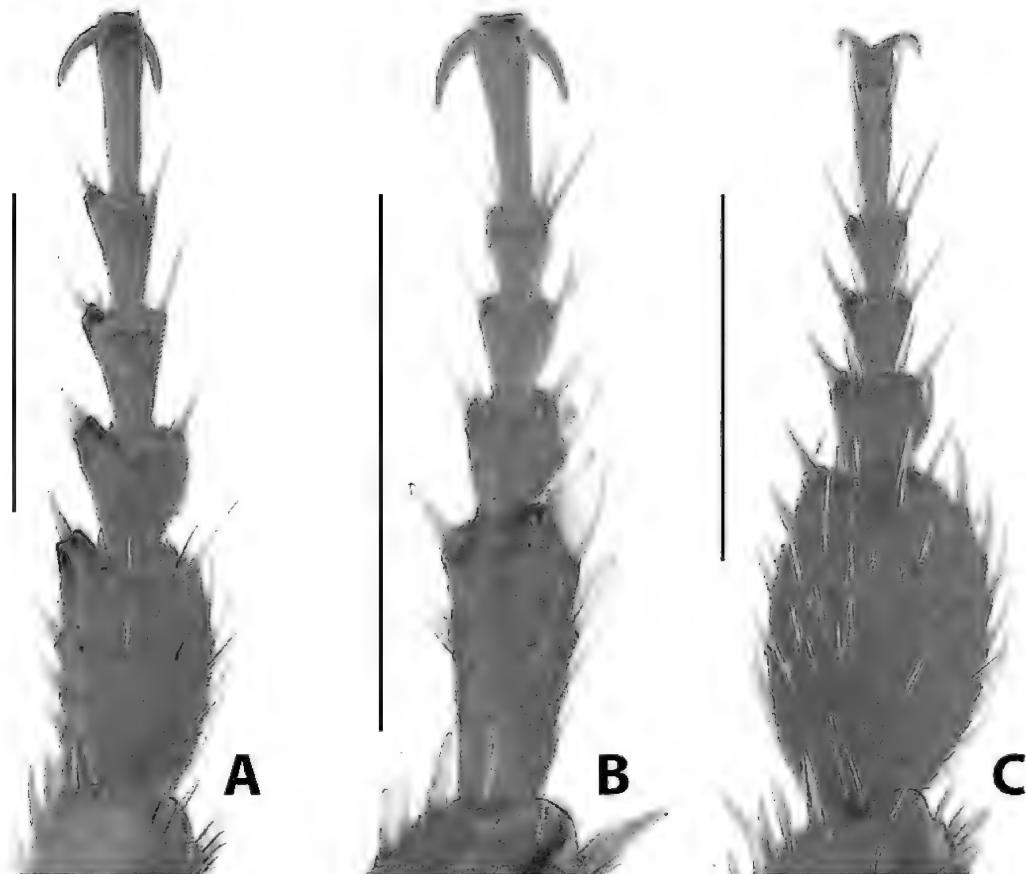


FIGURE 8. Male left protarsi of *Omophron* species, dorsal aspect. A. *O. pseudotestudo* Andrewes (CASENT1012676; Longchuan Jiang, Wuhe Township, Tengchong County, Yunnan, China); B. *O. gemneum* Andrewes (CASENT1012798; Xiaojiangqiao, Qushi Township, Tengchong County, Yunnan, China); C. *O. chelys* Andrewes (CASENT1016031; Dulong Jiang at Xianjiudang village, Gongshan County, Yunnan, China). Scale line = 0.5 mm

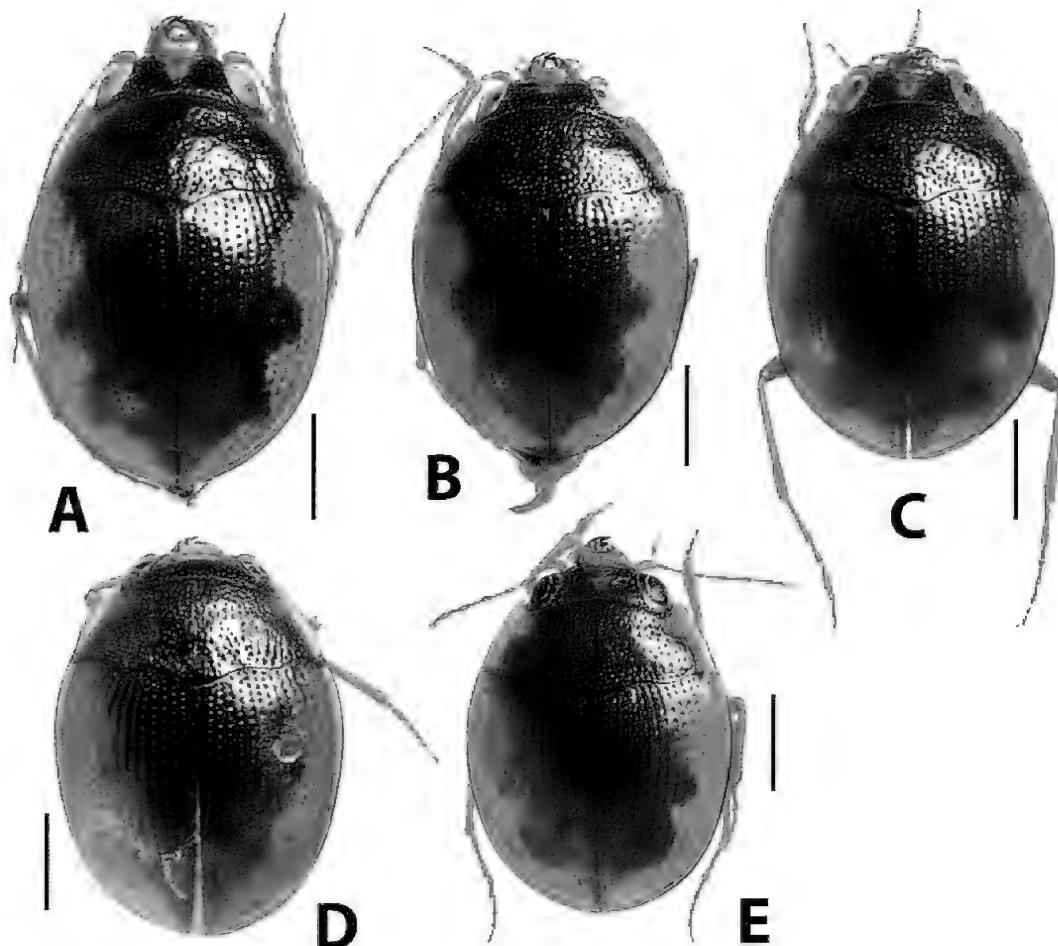


FIGURE 9. Dorsal habitus of *Omophron* species. A. *O. gemmeum* (CASENT1038994; Longchuan Jiang at Xiaojiangqiao, Tengchong County, Yunnan, China); B. *O. gemmeum* (CASENT1038992; Longchuan Jiang at Xiaojiangqiao, Tengchong County, Yunnan, China); C. *O. gemmeum* Andrewes (Holotype; West Almora District, Uttarakhand, India); D. *O. parvum* Tian & Deuve (Holotype; Jianhong, Xishuangbanna, Yunnan, China); E. *O. brettinghamae* Pascoe (5 km W of Rampur, Gunganagar, Chitwan, Nepal). Scale line = 1.0 mm.

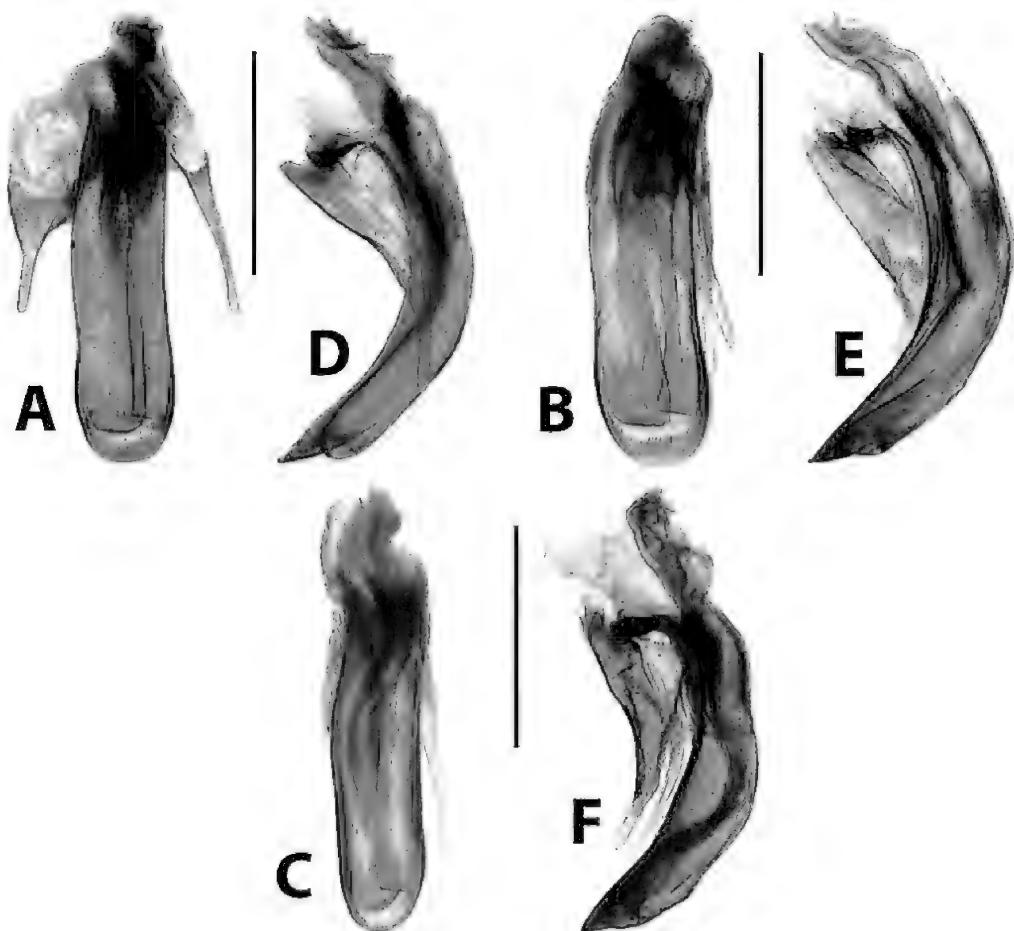


Figure 10. Male genitalia of *Omophron* species. A-C, dorsal aspects; D-F, left lateral aspect. A,D, *O. gemmeum* Andrewes (CASENT1038994; Longchuan Jiang at Xiaojiangqiao, Tenchong County, Yunnan, China); B,E, *O. gemmeum* (Holotype; West Almora District, Uttarakhand, India); C,F, *O. brettinghamae* Pascoe (Dinajpur, Bangladesh). Scale line = 0.5 mm.

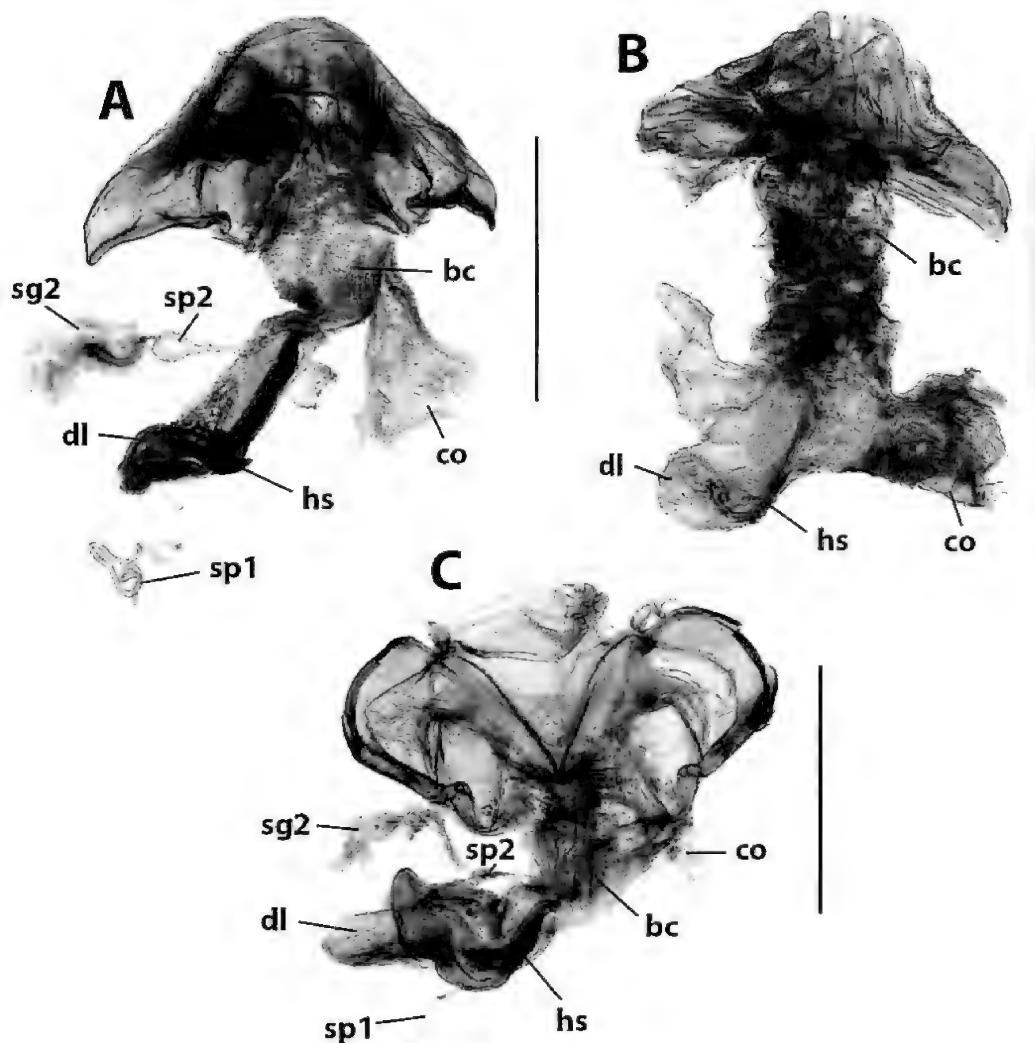


FIGURE 11. Female reproductive tract (dorsal aspect) of *Omophron* species. A. *O. gemmeum* (CASENT1039000; Longchuan Jiang at Xiaojiangqiao, Tenghong County, Yunnan, China); B. *O. gemmeum* (Holotype of *O. parvum* Tian & Deuve; Jianhong, Xishuangbanna, Yunnan, China); C. *O. brettinghamae* (Dinajpur, Bangladesh); bc = bursa copulatrix; co = common oviduct; dl = dorsal lobe of spermathecal; hs = helminthoid sclerite; sg2 = spermathecal gland 2; sp1 = spermatheca 1; sp2 = spermatheca 2 (sensu Liebherr & Will 1998). Scale line = 0.5 mm.

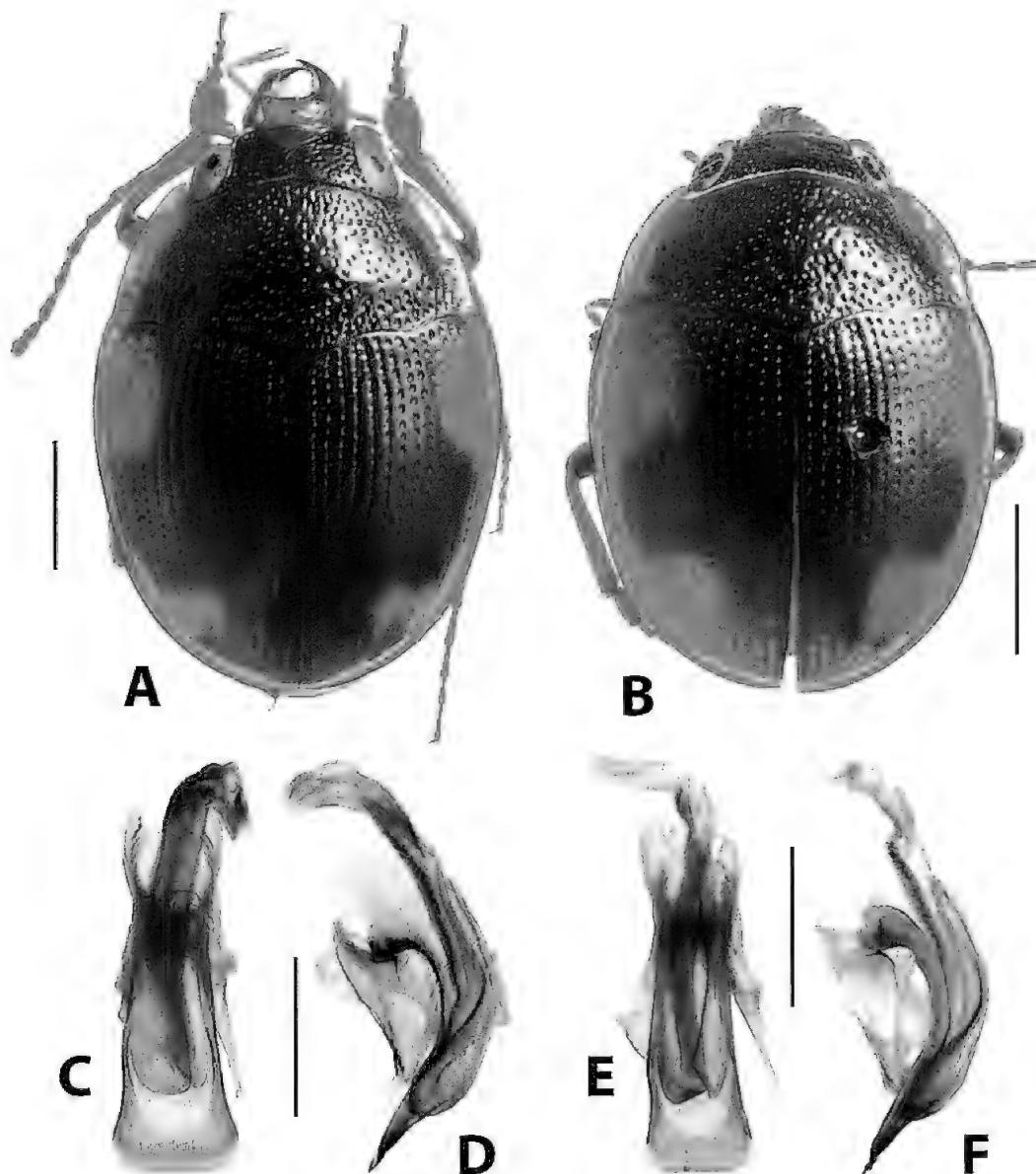


FIGURE 12. *Omophron chelys* Andrewes. A-B. Dorsal habitus. C-F. Median lobe of male genitalia; C,E, dorsal aspect; D,F, left lateral aspect. A,C-D. CASENT1016031 (Dulong Jiang at Xianjiudang village, Gongshan County, Yunnan, China); B,E-F. Holotype (Gopaldhara, Sikkim, India). Scale line A-B = 1.0 mm, C-G = 0.5 mm.

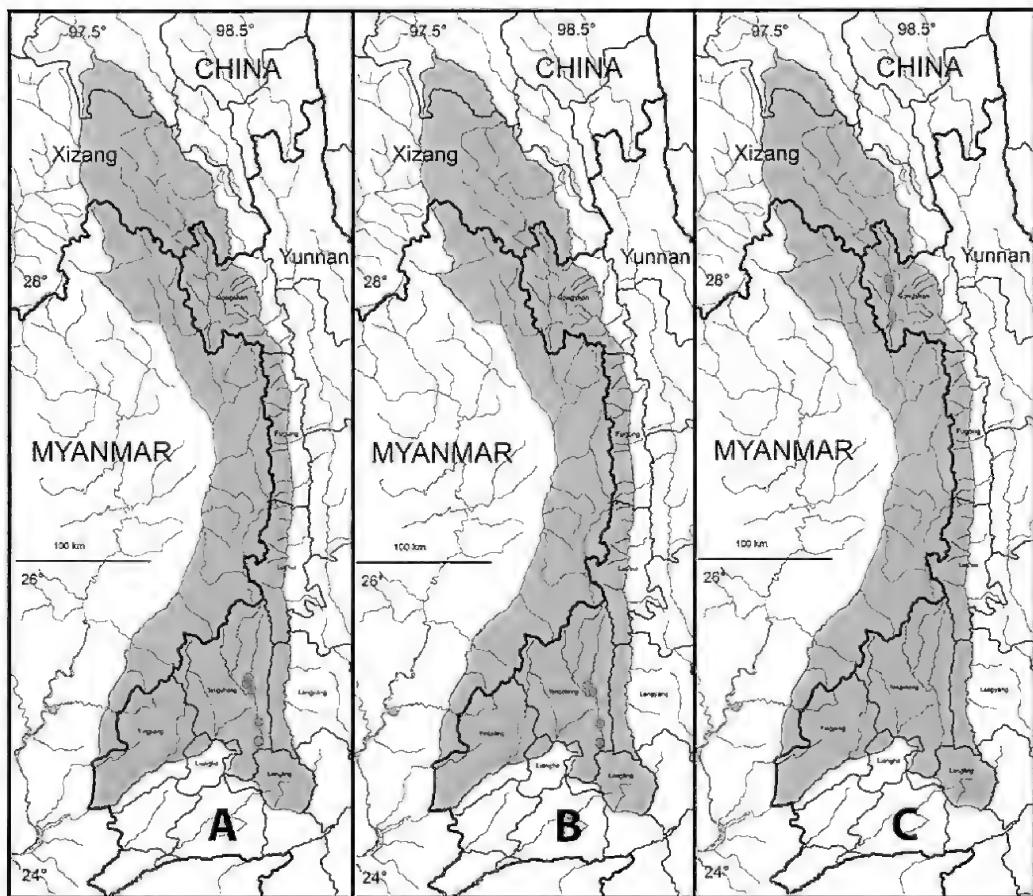


FIGURE 13. Maps showing locality records (red circles) for *Omophron* species in the Gaoligong Shan region. A. *O. pseudotestudo* Andrewes; B. *O. gemmeum* Andrewes; C. *O. chelys* Andrewes. Scale line = 100 km.



FIGURE 14. Photographs of habitats for *Omophron* species in the Gaoligong Shan region. A. Longchuan Jiang at Xianjiangqiao, Tengchong County, Yunnan, China (habitat for *O. gemmeum* Andrewes and *O. pseudotestudo* Andrewes); B. Dulong Jiang at Xianjiudang village, Gongshan County, Yunnan, China (habitat for *O. chelys* Andrewes). Photos by David H. Kavanaugh

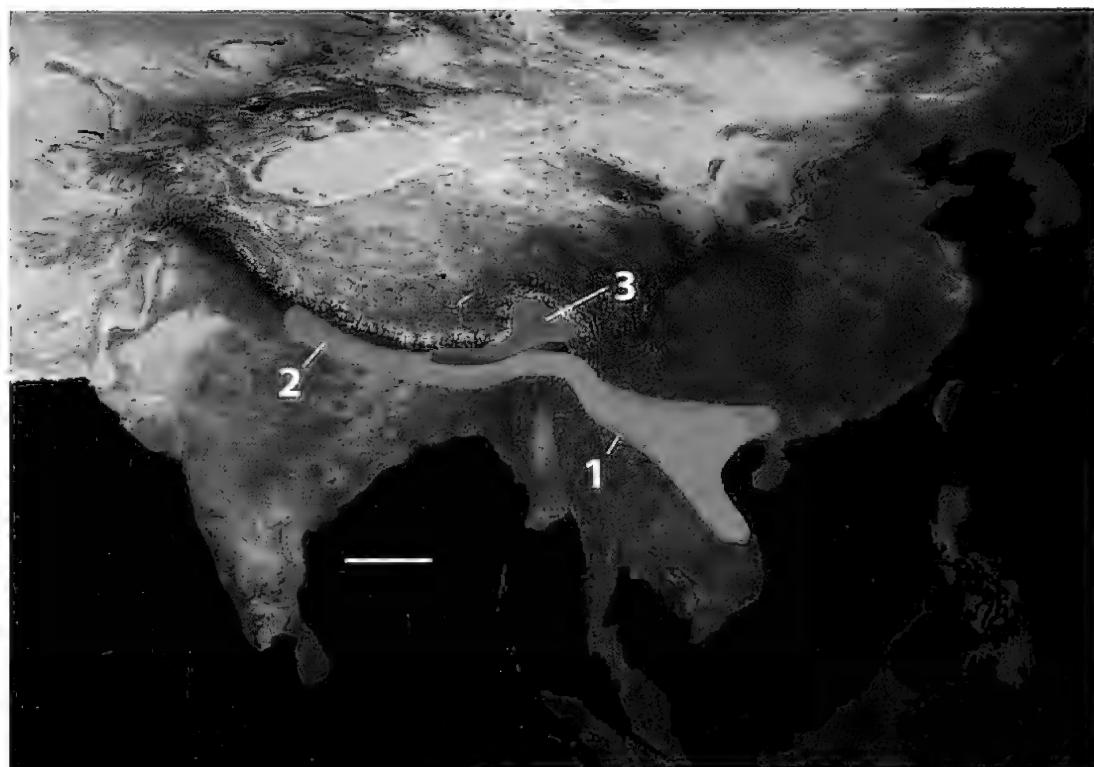


FIGURE 15. Map showing approximate known overall geographical distributions of *Omophron* species occurring in the Gaoligong Shan. 1. *O. pseudotestudo* Andrewes; 2. *O. gemmeum* Andrewes; 3. *O. chelys* Andrewes; Modified from Wikipedia Commons, World Atlas of the World, at URL: <http://upload.wikimedia.org/wikipedia/commons/8/8f/World_atlas_-_land_and_oceans_12000.jpg>. Scale line = 500 km.

ADDITIONAL OMOPHRON SPECIES KNOWN TO OCCUR IN CHINA

In addition to the three *Omophron* species known from the Gaoligong Shan region, another six species now are known to occur elsewhere in China. Adult specimens of the nine Chinese *Omophron* species can be distinguished using the following key.

Key for identification of adults of *Omophron* species known to occur in China

- 1 Elytra each with 15 striae, all deeply impressed throughout; pronotal dark area (Figs. 5A-B and 16A-E) not extended to near lateral explanations and either not extended to basal margin or extended to the basal margin only in the medial half 2
- Elytra each with 13 to 15 striae, all moderately or shallowly impressed, lateral striae more shallowly impressed and all striae apically less evident or effaced and represented only by punctures; pronotal dark area (Figs. 9, 12A-B, 16F) extended to lateral explanations or nearly so and broadly extended to the basal margin in medial three-fourths. 7
- 2 Size small, body length (BL) of males or females less than 4.5 mm; elytral intervals distinctly convex, striae coarsely punctate, elytral maculation pattern as in Figs. 16A-B; median lobe of male genitalia as in Figs. 17A-B,E-G. *O. stictum* Andrewes
- Size large, BL of males or females greater than 5 mm; elytral intervals flat to moderately convex, striae moderately punctate, elytral maculation pattern as in Figs. 5A-B, 16C-E; median lobe of male genitalia as in Figs. 6A-B,D-E, 17C-D,H-I 3
- 3 Antennomere 1 with two apical setae, antennomeres 3 and 4 with several setae laterally in addition to apical setal whirl; elytral intervals with a midline row of very fine, shallow punctures, elytral maculation pattern as in Figs. 5A,B; abdominal ventrite 5 setose; median lobe of male genitalia as in Figs. 6A-B,D-E; helminthoid sclerite of female reproductive tract as in Figs. 7A-B,D. *O. pseudotestudo* Tian & Deuve
- Antennomere 1 with a single apical seta, antennomeres 3 and 4 without lateral setae (i.e., with apical whirl of setae only); elytral intervals without midline row of punctures, maculation pattern as in Figs. 16C-E; abdominal ventrite 5 with a single pair of apical paramedial setae. 4
- 4 Elytral maculation pattern (Figs. 16D) with basal transverse band very narrow on intervals 4 to 7, distinctly broader on intervals 8 and 9, virtually absent from interval 10 to humerus (except for very narrow brown extension toward humerus in some specimens), metallic reflection of the basal band not extended laterally beyond interval 9; median lobe of male genitalia as in Figs. 17C,H; helminthoid sclerite of female reproductive tract as in Fig. 18B *O. rotundatum* Semenov
- Elytral maculation pattern (Figs. 16C,E) with basal transverse band very narrow on intervals 4 to 7, distinctly broader on intervals 8 to 13 and tapered to near humerus, metallic reflection of the basal band extended laterally at least to interval 13. 5
- 5 Silhouette (dorsal aspect) only slightly angulate at junction of pronotum and elytra, forebody only slightly narrower than elytra; pronotum with lateral explanation broad and impunctate or nearly so; elytra relatively narrow and elongate and only slightly expanded posterior to humerus, elytral intervals flat, elytral maculation pattern as in Tian & Deuve (2000; Fig. 10); median lobe of male genitalia as in Tian & Deuve (2000; Fig. 21) *O. hainanense* Tian & Deuve
- Silhouette (dorsal aspect) distinctly angulate at junction of pronotum and elytra, forebody clearly narrower than elytra; pronotum with lateral explanation narrow, sparsely punctate; elytra relatively short broad, distinctly expanded posterior to humerus, elytral intervals slightly convex, elytral maculation pattern as Figs. 16C,E; median lobe of male genitalia not as above 6

6 Elytral maculation pattern (Fig. 16C) with subapical transverse band connected to medial longitudinal band; median lobe of male genitalia as in Tian & Deuve (2000; Fig. 22) *O. aequale jacobsoni* Semenov

— Elytral maculation pattern (Fig. 16E) with subapical transverse band not connected to medial longitudinal band and separated from it by a gap of from one to four intervals, in most specimens represented as a separate spot or short chevron; median lobe of male genitalia as in Figs. 17D,I; helminthoid sclerite of female reproductive tract as in Fig. 18C. *O. saigonense* Chaudoir

7 Elytra each with 15 striae, stria 14 extended onto apical one-half; BL of males 4.5 to 5.3 mm, of females 5.0 to 5.7 mm; dorsum dark brown, without metallic reflection; pronotal and elytral lateral explanations broad; elytral maculation pattern as in Fig. 16F; median lobe of male genitalia as in Wrase (2002; Figs. 2-3) *O. piceopictum* Wrase

— Elytra each with 13 to 15 striae, if 15, then stria 14 extended only to basal one-third; BL of males or females 4.5 mm or less; dorsum dark brown to piceous, with or without metallic reflection; pronotal lateral explanation broad, elytral lateral explanation narrower at least in apical half; elytral maculation pattern as in Figs. 9A-D, 12A; median lobe of male genitalia as in Figs. 10A-B,D-E, 12C-D 8

8 Male protarsomere 1 greatly enlarged (Fig. 8C), distinctly wider than apex of mesotibia and longer than tarsomeres 2 to 4 combined; male mesotarsomere 1 also enlarged, as wide as mesotibial apex; elytra each with 15 striae near base, but striae 14 joined with stria 15 in basal one-third; dorsal dark areas dark brown, without metallic reflection, elytral silhouette slightly elongate, widest at basal one-fifth, elytral maculation pattern as in Fig. 12A; median lobe of male genitalia as in Figs. 12C-D; helminthoid sclerite of female reproductive tract as in Fig. 18A *O. chelys* Andrewes

— Male protarsomere 1 only slightly enlarged (Fig. 8B), narrower than apex of tibia and about as long as tarsomeres 2 to 4 combined; male mesotarsomere 1 only slightly enlarged, narrower than mesotibial apex; elytra each with 13 striae (striae 1 to 12 and 15) at basal one-third, striae 13 and 14 each present only as one to four punctures in basal one-fifth; dorsal dark areas with bright green or blue-green metallic reflection, elytral silhouette slightly shorter and more rounded, widest at basal one-fourth, elytral maculation pattern as in Figs. 9A-D; median lobe of male genitalia as in Figs. 10A-B,D-E; helminthoid sclerite of female reproductive tract as in Figs. 11A-B *O. gemmeum* Andrewes

4. *Omophron aequale jacobsoni* Semenov, 1922

Figures 16C, 19

Omophron aequale Morawitz, 1863:6. Type [not seen] deposited in ZIN. Type locality: Japan, Hokkaido, Hakodate.

Omophron jacobsoni Semenov, 1922b:46. Lectotype [not seen] in ZIN. Type locality: Russia, Primorsky Krai, Dal'negorskii District, Rudnaya River at Monomakhovo village.

Omophron jacobsoni mongolicum Semenov, 1922b:47. Holotype [not seen], a male, in ZIN. Type locality: Mongolia, Dornod Province, Buir Lake.

Geographical distribution in China. This species is widespread in China and has been recorded from Guangdong, Guangxi, Hainan, Jiangsu, Nei Mongolia, Ningxia, Shaanxi, Shanxi, Sichuan, Yunnan (Valainis 2013) and Zhejiang, although we have not examined any specimens from Yunnan.

Overall geographical distribution. (Fig. 19). The known range of this subspecies includes, in addition to the regions of China noted above, Mongolia, North Korea and South Korea. The

nominate subspecies, *O. aequale aequale*, appears to be restricted to Japan and Sakhalin Island (Russia). The record for Yunnan represents the westernmost limit to the known distribution of this species.

5. *Omophron hainanense* Tian & Deuve, 2000

Figure 19

Omophron hainanense Tian & Deuve, 2000:70. Holotype [not seen], a male, deposited in SCAU. Type locality: China, Hainan Island.

Notes on nomenclature and types. Although we have not had the opportunity to examine the unique holotype specimen of *O. hainanense*, its form and features as described and illustrated by Tian & Deuve (2000) support its recognition as a distinct species. We relied on features noted in the original description for recognition of this species in our key for species identification.

Geographical distribution in China. This species is known only from Hainan Island, the type locality.

Overall geographical distribution. (Fig. 19). Known only from Hainan Island, China.

6. *Omophron piceopictum* Wrase, 2002

Figures 16F, 19

Omophron piceopictum Wrase, 2002:772. Holotype [not seen], a male, in DWW [two paratypes examined]. Type locality: China, Sichuan, Ya'an Prefecture, Baoxing County, Jiajin Shan, river valley 3 km S of Qiaopi and 78 km NNW of Ya'an, 30.66667°N/ 102.75°E, 1950 m.

Geographical distribution in China. This species is known mainly from a few localities in central Sichuan, along the eastern base the mountain ranges forming the western rim of the Sichuan Basin. There are also nine specimens of this species in IOZ from Chengzhai, Xishui County, Guizhou Province, which is an area more than 300 km southeast of the nearest locality for the species in Sichuan.

Overall geographical distribution. (Fig. 19). Known only from Sichuan and Guizhou Provinces, China.

7. *Omophron rotundatum* Chaudoir, 1852

Figures 16D, 17C,H, 18B, 19

Omophron rotundatum Chaudoir, 1852:101. Type [not seen] deposited in MNHN. Type locality: "Mesopotamia" (which now includes Iraq, Kuwait and part of Turkey).

Geographical distribution in China. This species is confirmed to occur in China only in the Tian Shan region of Xinjiang Province in extreme western China. Andrewes (1929) recorded this species from "Annam" (Vietnam) and "Fokien" (Fujian Province, China) but noted that specimens from these areas had a more expanded pale color pattern than those from the main (and broadly disjunct) range of the species far to the west. Tian & Deuve (2000) recorded this species from Hainan Island, again with some reservation. As noted by Valainis (2010b), Kryzhanovskij (1982) concluded that the southeastern Asian records of Andrewes for *O. rotundatum* probably represent instead *O. saigonense*. We agree with Kryzhanovskij's assignment for both the Andrewes records and the Tian & Deuve record from Hainan Island. All the illustrations, of both external and internal genitalic features, provided by Tian & Deuve for the Hainan specimen correspond very well with the same features of *O. saigonense* adults (Figs. 16E, 17D,I and Fig. 18C) and not with those of typical *O. rotundatum* adults (Figs. 16D, 17C,H and Fig. 18B).

Overall geographical distribution. (Fig. 19). The geographical range of this species extends from Armenia and Iraq in the west, eastward the Tian Shan region in western Xinjiang (China) and western Uttarakhand (India), north into Kazakhstan and south into Afghanistan and Pakistan. The Tian Shan record from China represents the northeasternmost confirmed record for this species.

8. *Omophron saigonense* Chaudoir, 1868

Figures 16E, 17D, 18B, 19

Omophron saigonense Chaudoir, 1868:57. Type [not seen] deposited in MNHN. Type locality: Vietnam, Saigon.

Geographical distribution in China. As noted above, it is quite clear that the specimen from Hainan Island attributed to *O. rotundatum* by Tian & Deuve (2000) represents instead *O. saigonense*. Although we have not examined the specimen reported from “Fokien” (Fujian Province) by Andrewes (1929), this likely also represents *O. saigonense*. If this is correct, then this species is also likely to occur in Guangdong Province and perhaps also in Guanxi Zhuang Autonomous Region.

Overall geographical distribution. (Fig. 19). The known geographical range of this species extends from southern and central Vietnam northeast to Hainan Island and probably also to Fujian Province, China.

9. *Omophron stictum* Andrewes, 1933

Figures 16A-B, 17A-B, E-G, 19

Omophron stictus Andrewes, 1933:99. Lectotype [examined] (Fig. 16A), here designated, a male, deposited in BMNH, mounted on a minuten on a fiber rectangular block with a male symbol attached and labeled: “LECTOTYPE” [white circular disk with dark blue edge]/ “TONKIN Lac Thô HOA-BINH A. DE COOMAN”/ “Ex. Coll. Fleutiaux”/ “Type” [red label]/ “*Omophron stictus* Andr. Type [handwritten] H.E. Andrewes det.”/ “H.E. Andrewes Coll. B.M. 1945-97.”/ “LECTOTYPE *Omophron stictus* Andrewes By SWNichols 1980” [white label with thin black rectangle surrounding text, words “LECTOTYPE” and “By” in red ink]/ “LECTOTYPE *Omophron stictus* Andrewes, 1933 designated by D.H. Kavanaugh, R.L. Brett & H.B. Liang 2018” [red label]. Paralectotypes (a total of two [both examined] in BMNH): one male, mounted as the lectotype and labelled: “PARALECTOTYPE” [white circular disk with pale blue edge]/ “LAOS Hat Tiang le 14.XII.1917 R. Vitalis de Salvaza”/ “bought from Vitalios de Salvaza 1928”/ “H.E. Andrewes Coll. B.M. 1945-97.”/ “PARALECTOTYPE *Omophron stictus* Andrewes desig SWNichols 1980” [red label with thin black rectangle surrounding text]; one female, mounted as the lectotype and labelled: “PARALECTOTYPE” [white circular disk with pale blue edge]/ “TONKIN COLLECTION LE MOULT”/ Ex Coll. Bänninger”/ “*Omophron stictum* Andr. Cotype [handwritten] H.E. Andrewes det.”/ “H.E. Andrewes Coll. B.M. 1945-97.”/ “PARALECTOTYPE *Omophron stictus* Andrewes desig SWNichols 1980” [red label with thin black rectangle surrounding text]. Each paralectotype now also bears the following label: “PARALECTOTYPE *Omophron stictus* Andrewes, 1933 designated by D.H. Kavanaugh, R.L. Brett & H.B. Liang 2018” [yellow label]. Type locality: Vietnam, Hòa-Binh.

Omophron yunnanense Tian & Deuve, 2000:70. Holotype [examined] (Fig. 16B), a male, deposited in SCAU. Type locality: China, Yunnan, Jinhong. NEW SYNONYMY.

Notes on nomenclature and types. We find no evidence that the lectotype and paralectotype designations (specimens so labeled) of S.W. Nichols were ever published, so we validate these type designations here.

Our comparisons of the type specimens of *O. stictum* and *O. yunnanense*, including features of external form and structure (Figs. 16A-B) as well as of male genitalia (Figs. 17A-B, E-G), revealed few differences between them, although there is slight variation in the extent of the elytral dark maculation pattern among specimens of both type series, the extremes of which are

seen in Figs 16A and 16B, and in the shape of the median lobe in males. The median lobe of the lectotype male of *O. stictum* is less recurved apicocentrally in lateral aspect (Fig. 17E) than that of the holotype of *O. yunnanense* (Fig. 17G); but a specimen from near the type locality of the latter exhibits an intermediate state of this feature (Fig. 17F). While the holotype of *O. yunnanense* and lectotype of *O. stictum* are similar in width of the median lobe in dorsal aspect, the median lobe is wider than in either type specimen in the intermediate specimen just mentioned (Fig. 17B). Hence, there appears to be variation both in the amount of ventral deflection of the apex and in width of the shaft of the median lobe in males of this species, all within a relatively restricted geographical area. Based on all the evidence, we proposed that these names be treated as synonyms, with *O. stictum* having priority.

Geographical distribution in China. This species is known only from a small area in central to southcentral Yunnan Province.

Overall geographical distribution. (Fig. 19). The known geographical range of this species extends from central and southern Yunnan Province, China, east into northern Laos and northcentral Vietnam.

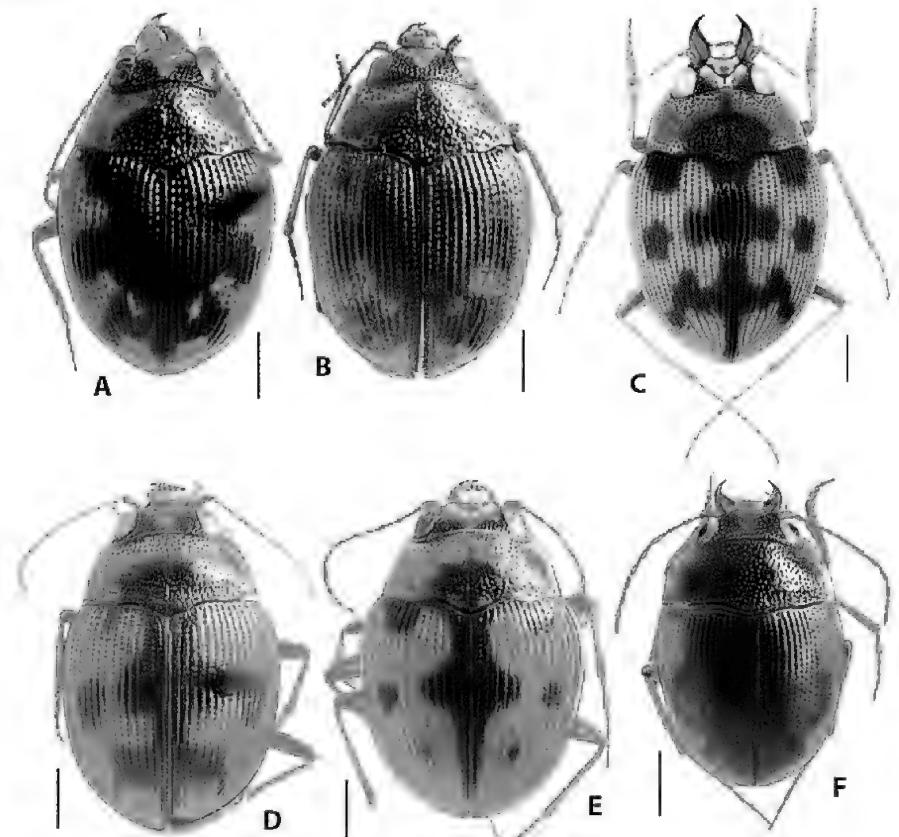


FIGURE 16. Dorsal habitus of *Omophron* species. A. *O. stictum* Andrewes (lectotype male; Hòa-Binh, Vietnam); B. *O. stictum* (holotype of *O. yunnanense* Tian & Deuve, Jinhong, Yunnan, China); C. *O. aequale jacobsoni* Semenov (Imbuk-ri, Yulgok-myeon, Hapcheon-gun, Gyeongsangnam-do, South Korea; modified from image on *Carabidae of the World* website, <<http://carabidae.org/taxa/aequale-jacobsoni-semenov-1922>>; copyright © Jong-Bong Choi); D. *O. rotundatum* Semenov (50 km S of Shahabad, Khorasan, Iran); E. *O. saigonense* Chaudoir (1.0 mile N of Quang Tri, Vietnam); F. *O. piceopictum* Wrase (paratype male; 3 km S of Qiaochi, Jiajin Shan, Baoxing County, Sichuan, China). Scale line = 1.0 mm.

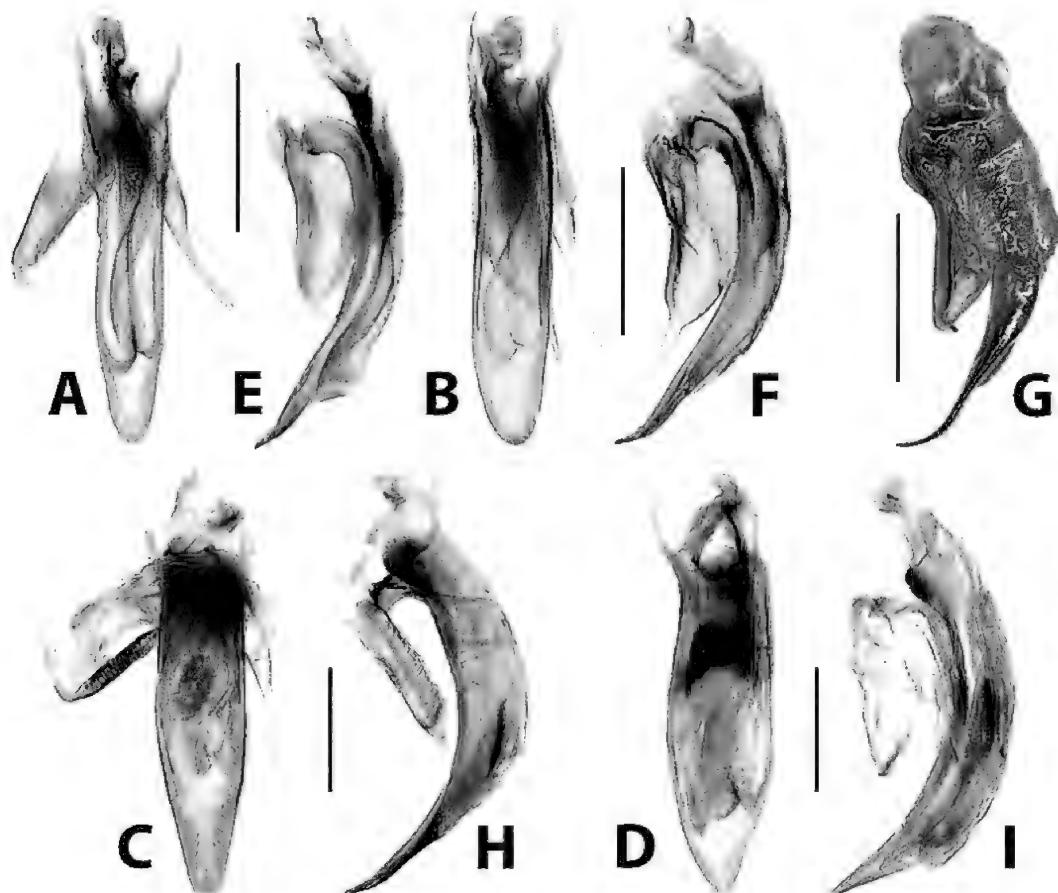


FIGURE 17. Male median lobe of male genitalia of *Omophron* species. A-D, dorsal aspect; E-I left lateral aspect. A,E, *O. stictum* Andrewes (paralectotype: Hat Tiang, Laos); B,F, *O. stictum* (CASENT8125453; Menglong, Jinhong, Xishuangbanna, Yunnan); C,H, *O. rotundatum* Semenov (45 km N of Ahwaz, Khuzistan, Iran); D,I, *O. saigonense* Chaudoir (1.0 mile N of Quang Tri, Vietnam); G, *O. stictum* (holotype of *O. yumanense* Tian & Deuve; Jinhong, Yunnan, China). Scale line = 0.5 mm.

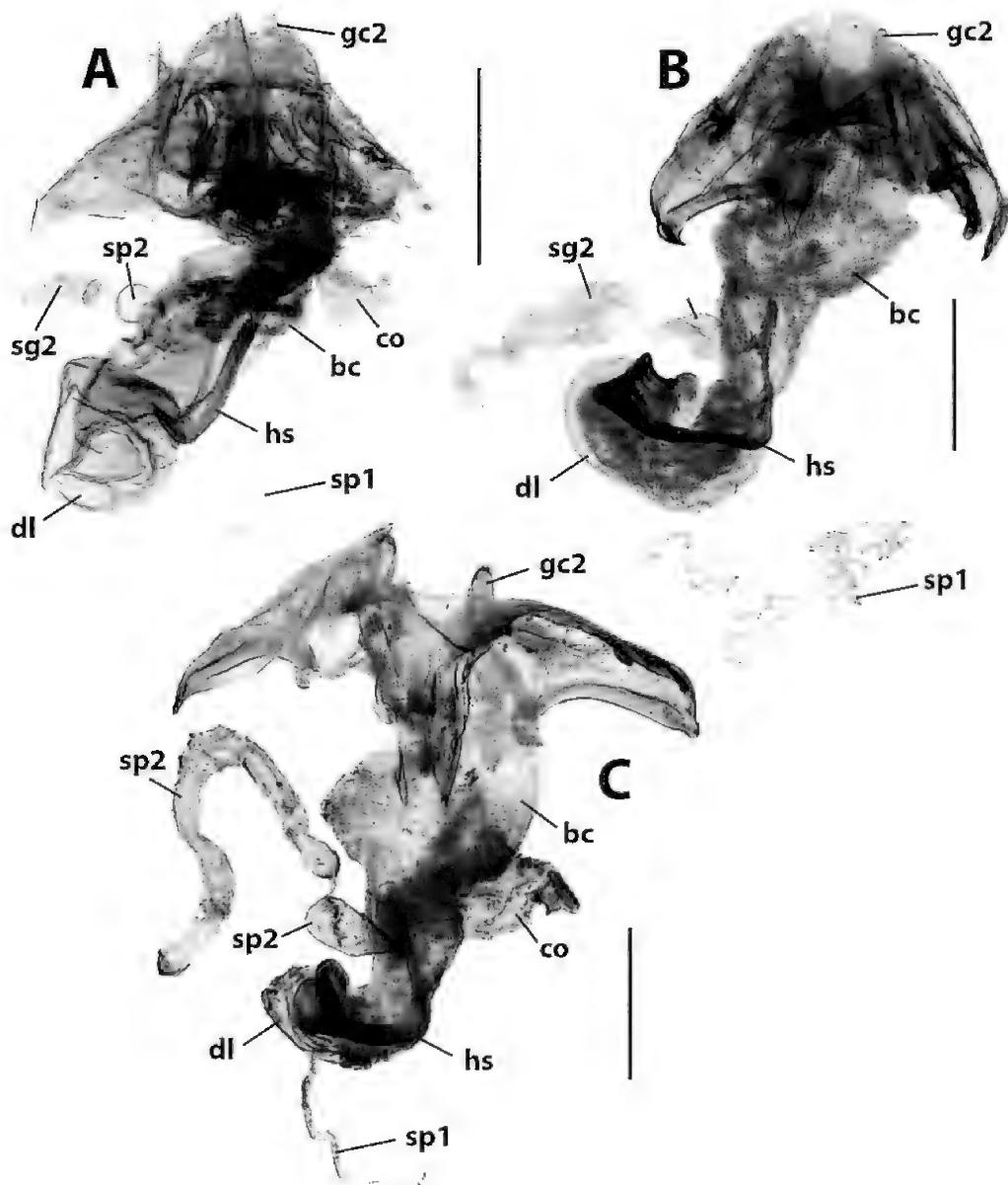


FIGURE 18. Female reproductive tract (dorsal aspect) of *Omophron* species. A. *O. chelys* Andrewes (CASENT1016093; Dulong Jiang at Elideng village, Gongshan County, Yunnan, China); B. *O. rotundatum* Semenov (Bukhara, Uzbekistan); C. *O. saigonense* Chaudoir (1.0 mile N of Quang Tri, Vietnam); bc = bursa copulatrix; co = common oviduct; dl = dorsal lobe of spermathecal; gc2 = gonocoxite 2; hs = helminthoid sclerite; sg2 = spermathecal gland 2; sp1 = spermatheca 1; sp2 = spermatheca 2 (sensu Liebherr & Will 1998). Scale line = 0.5.

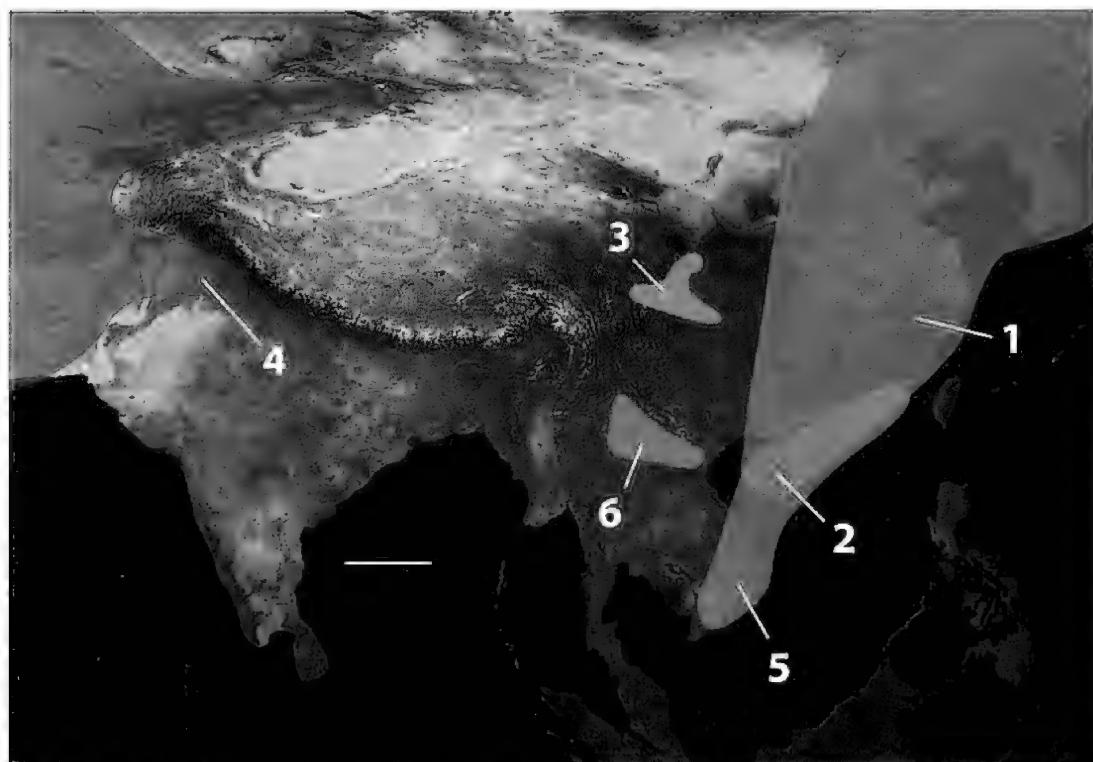


FIGURE 19. Map showing approximate known overall geographical distributions of *Omophron* species occurring outside the study area in China. 1. *O. aequale jacobsoni* Semenov; 2. *O. hainanensis* Tian & Deuve; 3. *O. piceopictum* Wrase; 4. *O. rotundatum* Semenov; 5. *O. saigonense* Andrewes; 6. *O. stictum* Andrewes. Modified from Wikimedia Commons, World Atlas of the World, at URL: <http://upload.wikimedia.org/wikipedia/commons/8/8f/Whole_world_land_and_oceans_12000.jpg>. Scale line = 500 km.

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William Anderson Newman

(November 13, 1927 – December 26, 2020)

In Memory of the Distinguished Invertebrate Zoologist,
and Mentor, Colleague, and Friend

John S. Buckeridge ¹, James T. Carlton ², Robert J. Van Syoc ³, Yair Achituv ⁴,
Raymond T. Bauer ⁵, Lene Buhl-Mortensen ⁶, Benny K. K. Chan ⁷, Giovanni Coletti ⁸,
Alberto Collareta ⁹, Mark J. Grygier ¹⁰, Michel E. Hendrickx ¹¹, Jens Thorvald Høeg ¹²,
Diana Jones ¹³, Francis Kerckhof ¹⁴, Tomas Kočí ¹⁵, Gregory A Kolbasov ¹⁶,
Jorge Laguna ¹⁷, Ray Perreault ¹⁸, Fábio B. Pitombo ¹⁹, Oleg P. Poltarukha ²⁰,
Roger W. Portell ²¹, Greg Rouse ²², Eve Southward ²³, Henry Spivey ²⁴,
Jon D. Standing ²⁵, John P. Wares ²⁶, and Toshiyuki Yamaguchi ²⁷

¹ Earth & Oceanic Systems Group, RMIT University, Melbourne, Victoria 3001, Australia; ² Williams College Maritime Studies Program, Mystic, Connecticut, Mystic, CT 06355 USA; ³ California Academy of Sciences, San Francisco, CA 94118 USA; ⁴ The Mina and Everard Goodman Faculty of Life Sciences, Bar Ilan University, Ramat Gan, Israel; ⁵ Department of Biology, University of Louisiana, Lafayette, LA 70504 USA; ⁶ Institute of Marine Research, Bergen, Norway; ⁷ Biodiversity Research Center, Academia Sinica, Taipei 115, Taiwan; ⁸ Dipartimento di Scienze dell'Ambiente e del Territorio e di Scienze della Terra, Università di Milano-Bicocca, 20126, Milano, Italy; ⁹ Dipartimento di Scienze della Terra, Università di Pisa, Pisa, Italy; ¹⁰ Center of Excellence for the Oceans, National Taiwan Ocean University, Keelung City, Taiwan (R.O.C.); ¹¹ Universidad Nacional Autónoma, Mazatlán, 82040 Sinaloa, Mexico; ¹² Department of Biology, University of Copenhagen, DK-2100, Copenhagen, Denmark; ¹³ Western Australian Museum, Welshpool WA 6106, Australia; ¹⁴ Royal Belgian Institute of Natural Sciences, 1200 Brussels, Belgium; ¹⁵ Palaeontological Department, National Museum, Prague 9, Czech Republic; ¹⁶ White Sea Biological Station, Moscow State University, Moscow, Russia; ¹⁷ Florida Department of Health, Tallahassee FL 32399 USA; ¹⁸ Jarreau Scientific, Baton Rouge LA 70805 USA; ¹⁹ Departamento de Biología Marinha, Universidade Federal Fluminense, Niterói, Brazil; ²⁰ A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia; ²¹ Florida Museum of Natural History, University of Florida, Gainesville FL 32611, USA; ²² Scripps Institution of Oceanography, La Jolla CA 92037 USA; ²³ Marine Biological Association of the UK, The Laboratory, Plymouth PL1 2PB, UK; ²⁴ Department of Biology, Coastal Alabama Community College, Gulf Shores AL 36542 USA; ²⁵ Lawrence KS 66049 USA; ²⁶ Department of Genetics, University of Georgia, Athens GA 30602 USA; ²⁷ Department of Earth Sciences, Chiba University, Chiba, Japan.

Correspondence: J. Buckeridge; e-mail: john.buckeridge@rmit.edu.au

William Anderson Newman passed away on December 26th 2020 at his home in La Jolla, California, aged 93. Bill spent much of his academic life at Scripps Institution of Oceanography, and also had a long and enduring association with the California Academy of Sciences. A marine biologist with deep interests in palaeontology and geology, Bill made spectacular contributions to the study of barnacles, including authoring 198 new taxa. But he is also remembered for his generous spirit, his mentorship and his support to emerging marine scientists.

Professor Emeritus William (Bill) Newman (Figs. 1, 2), born in San Francisco, California, on November 13, 1927, died peacefully at his home in La Jolla, California on December 26, 2020. Bill was 93. He is survived by his wife Lynn of La Jolla, sister Barbara Newman Witter of San Francisco, California, sons William Newman of Atascadero, California, James Newman of Pacific Grove, California, and Eric Newman of Viroqua, Wisconsin, daughter Doris Newman Horton of Kirkwood, Missouri, stepson Scott Kennedy of Lake Arrowhead, California, and 12 grandchildren.

Although he had been experiencing health problems over the last 18 months, Bill was, until the end, very active as a scientist, corresponding with colleagues until mid-December. During 2020 he published two articles and had further papers in preparation with colleagues or under review. Bill had been at Scripps Institution of Oceanography (SIO), at La Jolla, continuously since 1965, as a faculty member and as Curator of Benthic Invertebrates. He retained these positions until his retirement in 2006, when SIO appointed him Emeritus Professor of Biological Oceanography, and continued to provide him with office and laboratory space.



FIGURE 1. Professor Emeritus William A. Newman/Photograph courtesy of Scripps Institution of Oceanography Archives, UCSD



FIGURE 2. 1. Bill and Lynn Newman at home in La Jolla, with Sparky the beagle (2010). 2. Bill working on *Amphibalanus* at his microscope at Scripps Institution of Oceanography (SIO) (2018). 3. Bill (left) with Robert Hessler (center) during Japanese Emperor Hirohito's visit to SIO (1975); the Emperor was also a marine biologist. 4. Bill on the Scripps Pier, his office and laboratory on the corner of the ground floor of Hubbs Hall (to his right) (2010). 5. Bill examining the "barnacle tree" *Ceba insignis* at Balboa Park, San Diego (2010). 6. Bill and Lynn with John and June Buckeridge (left) and Bob and Amy Van Syoc (right) at Land's End, San Francisco, California (2014). 7. Bill at SIO - the Scripps Pier in the background (circa 2005). 8. Bill (circa 1978). Photographs 1, 4, 5, and 6 by John Buckeridge; photo 2 by James Carlton; photos 3 and 7, SIO archives; photo 8 by Arnold Ross.

Bill was foremost a marine biologist, although his interests and publications extended beyond biology to include palaeontology and geology. But it is within one field of marine biology that he made a spectacular contribution: cirripedology, or the study of barnacles. There can be no disagreement that Bill's work on the biology, ecology, biogeography, taxonomy, evolution, and phylogeny of barnacles constitutes the greatest contribution of any scientist in this field since Charles Darwin. But Bill was not solely a researcher. It was his enthusiastic and generous mentorship of emerging cirripedologists from across the globe that will also be one of his greatest legacies. He was indeed a giant amongst marine biologists, and was always prepared to have young zoologists stand on his shoulders and solve the riddles that eluded prior generations.

EARLY DAYS

Bill's magnetic attraction to the natural world, growing up in the Marina District on the shores of San Francisco Bay, began when he was barely post-larval. He recalled an incident when, as a very young child, a woman neighbor discovered him early one morning at the Palace of Fine Arts feeding the ducks, and promptly escorted him home to be presented to his mother. "Young Billy" apparently attracted notice, in part, because he was still in his pajamas. Bill often recalled fondly going down to the docks – these were the Depression Years of the early 1930s – getting some pile worms for bait from a local fishmonger, and then fishing with the old men who would tell him the names of what he had caught. Bill would lie on the dock and look at the pilings underneath and "the little critters sticking their heads out" (Newman, 2012). The little critters were barnacles.

The family would take the ferry across the Golden Gate north to Sausalito – before there was a Golden Gate Bridge – and Bill would wander about the tide pools and collect shells. The family also sailed on San Francisco Bay, where Bill learned to race in an International 14, a 4.3 meter double-handed dinghy. Sailing continued as a passion for the rest of Bill's life – "boats have always been in my blood" (Newman, 2012). In 1943, when Bill was only 15 years old, one of his teachers wrote that, "For Bill, every blade of grass, every strange noise, every phenomenon of nature and science hold a fascination."

From age 18 to 20 Bill served two years in the United States Army, following which there was a brief stint at a junior college a half-hour south of San Francisco. Although he earned an Associate's Degree, college was not to Bill's immediate taste, and he spent the next two years or so learning to build boats in Sausalito, a skill which he would put to good use a decade later in the Caroline Islands.

UNIVERSITY

By the fall of 1948 Bill was back in college, enrolled at the University of California at Berkeley (UCB), majoring in Zoology. In due course he took the late Professor Ralph I. Smith's invertebrate zoology class and then spent the summer of 1952 furthering his invertebrate knowledge in a course taught by Professor Smith and the late Professor Cadet H. Hand, Jr. at Hopkins Marine Station in Pacific Grove, California. Bill earned his Bachelor of Arts degree in 1953, and a year later a Master of Arts, with Smith as advisor, exploring the ecology and distribution of barnacles in San Francisco Bay (Newman, 1954).

Bill's captivation with invertebrates, and specifically barnacles, was thus cemented in his undergraduate and earliest graduate days at Berkeley. In a letter of June 6, 1972, Bill wrote to Smith that Ralph was "directly responsible in getting me interested in invertebrate zoology rather than terrestrial vertebrates or fishes. I hope you are happy with what you did – I am!" On March 23, 2001, Bill sent a reprint of his and Arnold Ross' 2001 paper, "Prospectus on larval cirriped setation for-

mulae, revisited,” to his other primary Berkeley mentor, Cadet Hand, adding a note that read, “With appreciation for introducing me to so much in invertebrate zoology, including Garstang (1954) – you gave me a copy of his book following Invertebrate Zoology 112 [that] I’d TA’d in the spring of 1954.” The opening quotation of Newman & Ross (2001) is from Garstang.

But again the lure of “doing something interesting,” as Bill described it, took him away from academia for two years (1954-1956), this time to the coral-rich Chuuk Lagoon (then Truk Atoll) in the tropical Western Pacific. Bill would recall his time there fondly for the rest of his life. He accepted a position to teach college preparatory classes to high school students at the Pacific Islands Central School, and with nearly every hour of his free time he immersed himself in learning about coral reef ecology, and, of course, studying Micronesian barnacles. With the aid of the school shop foreman, Bill built a 3.7 meter boat, intentionally broad (1.4 meters!) to safely explore the lagoon and islands. For added comfort, Bill added a weather cockpit made from an old truck windshield and a canvas top. It was, said Bill, “a delightful little boat,” and he collected the island and sea life extensively, from lizards and fish to mollusks and crustaceans (Newman, 2012).

Bill returned to Berkeley at the age of 30 and was accepted into the PhD program in Zoology in 1957. Having invested interim years in boat building and in teaching, he was several years older than his fellow matriculants. As a result, Bill was a *rara avis*, bringing to his graduate studies a level of marine biological experience and maturity that doubtless quickly set him apart from his cohort. It was then that he first met the late Victor Zullo, a new graduate student in Palaeontology at UCB, who was to become a close friend and colleague, and a fellow cirripedologist, until Zullo’s untimely passing in 1993. Coincidentally, Vic had also been born in San Francisco and similarly had grown up, as had Bill, in the Marina District.

While a grad student at UCB, Bill’s broader interest in marine arthropod evolution was stimulated by the late Meredith Jones’ discovery of the second species of Cephalocarida, *Lightiella serendipita* Jones, 1961, in sediment samples dredged from San Francisco Bay. Bill had an opportunity to examine the odd find under a microscope and was fascinated. The connection to Cephalocarida continued much later in his career as Bill and the late Bob Hessler, who studied with Howard Sanders (the describer of the first cephalocaridan), later co-taught a survey class of Marine Arthropods to their many grad students at Scripps.

With hardly one foot in the door at Berkeley, in the summer of 1958 Bill accepted an offer to spend a week sampling San Diego Bay in southern California in connection with an appraisal of the impacts of sewage discharge (Newman, 1958) – a week well spent, as it turns out, not simply to earn a bit extra to support his young family, but Bill later noted that his brief study (while “eating pizza for breakfast and lunch left over from dinner”) attracted the attention of scientists at Scripps, who, just a few years later, would be seeking a collections manager for benthic invertebrates.

Bill completed his doctoral dissertation, “Adaptive behavior and physiology of estuarine barnacles,” in 1962. His thesis committee consisted of Cadet Hand, Ralph Smith, the late J. Wyatt Durham, and the late Frank A. Pitelka. Bill focused his work on the physiology and distributional ecology of three species of barnacles in San Francisco Bay, the native *Balanus glandula* Darwin, 1854, the non-native *Balanus improvisus* Darwin, 1854 and *Balanus amphitrite* Darwin, 1854 (the latter two now in the genus *Amphibalanus*). Bill’s work was the first to explore the biology and ecology of introduced barnacles in the Eastern Pacific Ocean. In those more halcyon academic days, Bill’s doctoral work was not to appear in print until 1967, published in a volume of the *Symposium on Crustacea*, which had been held in 1965 in Ernakulam, India.

ACADEMIC CAREER

Upon graduation, Bill was offered a position as an invertebrate curator at Scripps. He bargained to be appointed (1962-1963) as Assistant Professor of Biological Oceanography as well. While he had a strong dislike for undergraduate teaching (seeded by having had to teach hundreds of students in a broad survey zoology course at Berkeley), he nonetheless wanted to teach at the graduate level, something he could not do solely as a curator. But Bill had also been offered a position at the same time at the Museum of Comparative Zoology at Harvard University, and after only a year he left Scripps to accept a position as an Assistant Professor of Zoology at Harvard, aided by the late Professor Ernst Mayr. Here Bill had a “wonderful experience,” meeting many New England scientists (including such luminaries as Howard Sanders at Woods Hole Oceanographic Institution, and where he worked again with Vic Zullo, then temporarily at the Marine Biological Laboratory in Woods Hole). But an apparent combination of financial (Newman, 2012) and cultural (Southward 1995) challenges caused Bill to reverse course after only two years at Harvard, and fortunately he was able to resume his former position at Scripps in the summer of 1965. Whether New England’s weather, to which Bill was not acclimatized, also played a factor we do not know, but Bill was clearly moved by the dramatic contrast between the rich intertidal life of California and the lower-diversity shores (“it was the dullest”) of New England (Newman, 2012).

Always in motion and with the boundless energy that was one of the striking hallmarks of his life, Bill managed to squeeze in a trip to Fanning Island in the summer of 1963, between leaving La Jolla and moving to Cambridge. As with Truk, his visit to Fanning, with his colleagues the late Stephen Wainwright and the late Charles Stasek, would generate memories that he would regularly return to for the rest of his career. Giving us pause today is Bill’s account of needing to learn SCUBA to fully explore Fanning: he and his colleagues purchased the necessary equipment in Hawaii, and then “We read the directions the gear provided” (Newman, 2012).

Bill returned to Scripps in the summer of 1965, and he never left. In 1997, Bill shifted to his office on the ground floor of the new Hubbs Hall, where he remained for the remainder of his magnificent 55-year career. And it was from this splendid location that he explored nearly every corner of the evolutionary history, biogeography, and systematics of barnacles.

An important early contribution was published in 1969, when Bill was joined by Vic Zullo (then at CAS) and the late Thomas Withers (British Museum of Natural History) in writing the section on barnacles in the prestigious *Treatise on Invertebrate Paleontology*. This contribution dealt with much more than just fossils: it brought together the then current knowledge on barnacle biology, biogeography, paleontology, phylogeny, and taxonomy. It remains an important reference for cirripedologists, for it included some inspired observations that changed the way in which barnacles were perceived. Many of these observations, especially those that led to the framework upon which barnacle phylogeny is based, are still essentially correct – even with the much greater advances of molecular genetics. Over the following decades, Bill’s contribution to the understanding of barnacles expanded to include publications that would serve a broader sector of the community: the Cirripedia sections in the *Encyclopaedia Britannica* (Newman, 1974, 1991), *Light’s Manual of Intertidal Invertebrates* (Newman, 1975, 2007), and *Intertidal Invertebrates of California* (Newman & Abbott, 1980).

In 1971, Bill and the late Arnold Ross published *Antarctic Cirripedia*, a monograph of more than 250 pages in which they described 20 new species, nine new genera, and a new family (comprising more than 15% of the taxa described by Bill in his entire career). This was a defining publication, in its approach and in its impact. Much emphasis was placed upon the global significance and distribution of Antarctic cirripedes, which had, up to that time, been poorly understood. Bill and Arnold were able to draw on material collected by all previous expeditions to the Antarctic, but

the comprehensive collections made by USNS *Eltanin* during her cruises in 1962–1965 provided the bulk of the specimens that underpinned the study’s insights. Over 85 species were treated, many of which had previously been poorly described and illustrated. This was effectively rectified in *Antarctic Cirripedia*, in which useful distribution charts, updated figures, and excellent identification keys amply complemented the (re)descriptions.

A year later Bill went on his first (and only) sabbatical to the Plymouth Marine Laboratory in the United Kingdom. During that year he published 11 research outputs (including two in conference proceedings), testifying to the value of the sabbatical – during which an absence of other duties, especially administrative, allowed his research to flourish. Bill’s host at Plymouth was the late Alan Southward, who had been working on British barnacles since the 1950s. They had met each other in 1963, when Alan introduced Bill to the Acrothoracica – a group of diminutive burrowing barnacles to whose taxonomy and substrate relations Bill contributed substantially later (Grygier & Newman, 1985; Newman 1996). Their love of barnacles led to a life-long friendship, during which they published a dozen papers together on barnacles.

It is an interesting parallel that an acrothoracican barnacle had also been instrumental in luring Charles Darwin into cirripedology. Like Darwin, Bill was interested in sea-level change, and barnacles were an excellent proxy to explore this. But it was also Bill’s fascination with Darwin, and the way that Darwin (1852, 1854) had intuitively mapped out an impressive barnacle classification – without the support of genetic sequence data – that led Bill to write a number of papers on Darwin’s contribution to carcinology (e.g. Newman 1993). One paper, co-authored with one of us (Buckeridge & Newman, 2010), demonstrated just how close to the truth Darwin was and showed that some subsequent changes by modern cirripedologists to Darwin’s original taxonomy were incorrect. This was rectified, with a revised system much closer to that proposed by Darwin. Bill loved this opportunity – to demonstrate how modern biologists, even with access to wonderful new technology, may still get it wrong. Nonetheless, Bill recognized early on that the existing classification was wanting, and over the decades he too proposed significant changes in the classification of barnacles. Many of these, such as the assignment of *Balanus balanoides* (Linnaeus, 1767) to *Semibalanus balanoides* were strongly resisted by other barnacle taxonomists (see Southward, 1995), but Bill persisted, and many of his changes are now accepted.

One of us (JB) recalls Bill’s participation in a symposium on the Marine Biogeography and Evolution in the Southern Hemisphere during the mid-1970s. At this meeting, held in New Zealand, he gave a robust presentation that would significantly revise the way in which the megabalanines, especially those endemic to New Zealand and Australia, would be classified (Newman, 1979). Local biologists were affronted that a visiting American had proposed a re-classification of their barnacles. However, after only two years, the Newman model was widely adopted. As he had done before, he had “shaken up” entrenched local ideas about barnacle classification and phylogeny, and his insightful concepts were, after some vociferous opposition, shown to be correct. It is significant that Bill’s enthusiasm and passion quickly led to collaborative research with Australasians, in particular with Diana Jones (Perth), John Buckeridge (Melbourne), and the late Brian Foster (Auckland). Indeed, a willingness to discuss differences in interpretation was a mark of the man. His “urbanity” (Southward, 1995) resulted in Bill’s influence rivalling that of the late Henry Pilsbry, the formidable American cirripedologist who had been based at the US National Museum.

Bill’s appreciation of the significance of barnacles in the biosphere, including how they can be used as proxies for environmental change and interpretation (as in paleoecology), was complimented by his ability to compile barnacle catalogues – a rather onerous task. The most significant of these is the comprehensive *Revision of the balanomorph barnacles; including a catalog of the species* (Newman & Ross, 1976), as this publication, now more than four decades old, remains for

many of us the “go to” global text when describing a new species and for checking the distribution and synonymies of existing taxa. It is most unfortunate that only the Balanomorpha were covered in this manner, despite an effort on Bill’s part to produce a companion volume on the stalked barnacles.

Bill returned frequently to several themes in his work. One was the taxonomy and host relations of symbiotic barnacles, some purportedly parasitic, including those attached to sea turtles, decapod crustaceans, echinoderms, bryozoans, sponges, and scleractinians and other corals, with particular attention to the pyrgomatid coral barnacles (the latter in collaboration with Arnold Ross). Another was his use of barnacles to address biogeographic themes such as endemism in coastal transition zones between major biogeographic provinces, amphitropicality, and endemism and peripheral isolation in the Southern Ocean and Eastern Tropical Pacific. Over a span of more than 50 years Bill was also interested in modern barnacle invasions as mediated by ship fouling, starting in the early 1960s with reporting *Amphibalanus eburneus* (Gould, 1841) from the Hawaiian Islands (Newman et al., 1964) and culminating in a review of introduced barnacles of the Americas (Carlton, Newman, and Pitombo, 2011).

Of great importance was the attention Bill devoted to hydrothermal vent barnacles in a monumental series of works from 1979 to 1997. The study of the origins and nature of ocean ridges began in earnest in the late 1960s, with Scripps being one of the founding institutions in this enterprise (Lonsdale, 1977). Like many of the organisms recovered beginning in the 1970s from hydrothermal vents along these spreading ridges, the barnacles were very unusual. They were returned to Scripps for analysis, where Bill’s knowledge of both living and fossil barnacles enabled him to recognise them as primitive taxa; he saw these new species as windows to the Mesozoic. These papers included descriptions of what Bill considered to be the most primitive living representatives of the Scalpellomorpha, Verrucomorpha, and Balanomorpha as well as the only extant brachylepadomophan, and detailed hypotheses as to how verrucomorphans and balanomorphans arose from brachylepadomorphans. This work was definitive in Bill’s demonstrating the influence of competition on the evolution and distribution of cirripedes (Newman & Stanley 1980; Southward, 1995). Later workers have shown that Bill’s conceptions of the phylogeny of different barnacle groups, although often sound in terms of actual morphological transitions (e.g. Glenner et al., 1995), was largely grade-based, not clade-based (e.g. Pérez-Losada et al. 2002). As a result, some of these vent taxa are now classified differently (e.g. Chan et al., in press), but their overall significance in understanding barnacle evolution remains undeniable.

Bill advised many graduate students over his decades at SIO, both his own and others. Bill gave his students the independence to develop their own lines of research, while providing the guidance necessary to help them overcome obstacles. Bill’s contact with his students often continued for years beyond their time at SIO. Several of Bill’s former students became collaborators on joint research projects that were developed in later years (e.g. Grygier & Newman, 1991; Newman and Gomez, 2003; Bauer & Newman, 2004; Van Syoc & Newman, 2010). Bill was also a valued mentor to legions of visiting cirripedologists, both emerging and long-established. Whether from another state or from overseas, visitors were provided laboratory space, and were generously supported with accommodation and fine meals, often at the Newman’s home in La Jolla. In 1978 Bill organized at Scripps the First International Workshop on Cirripedia, which was attended by both junior and senior barnacle workers, including Dennis Hedgecock, the late Dora Henry, Cindy Lewis, the late Patsy McLaughlin, the late Arnold Ross, Henry Spivey, the late Alan Southward and Jon Standing.

CALIFORNIA ACADEMY OF SCIENCES: A LONG AND ENDURING ASSOCIATION

Bill Newman held a very special place in his heart for the California Academy of Sciences, and throughout his long career deeply valued knowing and working with the Academy's invertebrate zoologists and paleontologists. One of Bill's earliest childhood memories, in the 1930s growing up in the City, was seeking help at the Academy, including Steinhart Aquarium, to identify his mollusk and other invertebrate discoveries from San Francisco Bay and the nearby coast. He referred vividly in an oral history at Scripps to being inspired as a budding naturalist by the Academy staff. By the early 1950s, Bill, now in his twenties, had become fascinated by barnacles, and was coming over to the Academy from UC Berkeley to study the barnacle collections — it was at this time that he met and discussed his findings with the late Frank Lee Rogers, an Academy Research Associate in Geology, and the only prior worker on San Francisco Bay barnacles (Rogers, 1949). Several years later Bill was working on the discovery in San Francisco Bay of the Oriental shrimp *Palaemon macrodactylus* Rathbun, 1902 (the Academy holds specimens collected by Bill whilst at Berkeley in 1961). In a seminal paper (Newman, 1963) he warmly thanks Earl Herald, Kenneth Innes, and Allyn G. Smith for allowing him to work in the Academy's shrimp collections, acknowledging that without their assistance and the Academy's collections he would not have been able to establish the timing of introduction of this shrimp into the Bay.

Importantly, Bill Newman was a long-term collaborator, for more than 50 years, with Academy scientists. He worked closely with the late Victor Zullo, publishing a half-dozen papers together, including when Vic was on the CAS staff from 1967-1971. From 1971-1974, Bill worked with one of us (JTC), then on the CAS staff, on invasive barnacles and, especially, on a barnacle chapter for the 1975 Third Edition of *Light's Manual*, which Jim co-edited. From 1979 to 2014, RVS was a member of the CAS curatorial staff; Bob was one of Bill's Ph.D. students, and he and Bill co-authored papers together from 1992 to 2015.

Bill also contributed material to the Academy's collections, including shrimp, barnacles from Puerto Rico, Truk, and elsewhere — and even ostracod crustaceans (the famous "horse-trough" species *Heterocypris incongruens* Ramdohr, 1808) that he collected in 1952 on the UC Berkeley campus. Type material of the Miocene barnacle *Zulloa imperialensis* Ross and Newman, 1976, is deposited at CAS — the only known specimen of this unique barnacle. And, of course, Bill's research also employed additional barnacle material held at CAS, including, in 2017, studying some of Frank Lee Rogers' San Francisco Bay barnacles, closing a more than 60-year loop!

EPILOGUE

Bill Newman's contribution to our understanding of Cirripedia was prodigious: over a period of 60 years he produced 150 papers (out of 198 publications; Appendix 1) and authored 198 new taxa (Appendix 2). Bill is also remembered in 15 currently recognized taxa named after him (Appendix 3). But for those of us lucky enough to have spent time with Bill in the field, it quickly became clear that there was more to Bill than barnacles — he had a great passion for the flora, fauna and geology of arid environments. However, it was in the relaxing time of an evening, that Bill's interest in fine food and wine, and of course an excellent malt whisky, shone through. In Appendix 4 we share further memories of Bill by many of the present co-authors. These remembrances, in aggregate, paint a picture of a colleague who will be dearly missed. Bill was not simply a fine scientist, he was a valued and supportive friend.

Vale WAN!

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Appendix

APPENDIX 1

Publications and Other Research Outputs (1958-2020) of William A. Newman

Theses

Newman, W.A. 1954. *Some ecological considerations on barnacles of the San Francisco Bay estuarine system*. M.A. thesis, University of California, Berkeley.

Newman, W.A. 1962. *Adaptive behavior and physiology of estuarine barnacles*. Ph.D. thesis, University of California, Berkeley.

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Newman, W.A. 1960. On the paucity of intertidal barnacles in the tropical Western Pacific. *Veliger* 2(4): 89-94.

Newman, W.A. 1960. Five pedunculate cirripeds from the Western Pacific, including two new forms. *Crustaceana* 1(2): 100-116.

Newman, W.A. 1960. *Octolasmis californiana*, spec. nov., a new pedunculate barnacle from the gills of the California spiny lobster. *Veliger* 3(1): 9-11.

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Newman, W.A. 1961. Notes on certain species of *Octolasmis* (Cirripedia, Thoracica) from deep sea Crustacea. *Crustaceana* 2(4): 326-329.

Newman, W.A. 1961. On certain littoral species of *Octolasmis* (Cirripedia, Thoracica) symbiotic with decapod Crustacea from Australia, Hawaii and Japan. *Veliger* 4(2): 99-107.

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APPENDIX 2

A chronological list of taxa named by William A. Newman

This list of 198 taxa is arranged chronologically. Of particular interest is the involvement of others as co-authors. For the first decade, Newman was, with the exception of *Lithoglyptes spinatus*, the sole author of any new species that he described. However, it is a mark of his growing status as a cirripedologist, and the opportunities for mentorship that this provided, that mark him as a collegial and supportive scientist. This mentorship and generosity of spirit is reflected in his publications over the last 20 years – with only three out of 49 lacking co-authors. Our designation of an accepted current name (as of February 2021) reflects its status in the World Register of Marine Species (<<http://www.marinespecies.org/>>).

Heteralepas utinomii Newman, 1960 (Withers, 1935)]
Octolasmis californiana Newman, 1960 [accepted as *Arcoscalpellum imbricotentum* Newman & Ross, 1971
Octolasmis lowei (Darwin, 1852)]
Paralepas palinura Newman, 1960 [accepted as *Paralepas palinuri* (Barnard, 1924)] *Arcoscalpellum latusculum* Newman & Ross, 1971 [accepted as *Teloscalpellum latusculum*]
Paralepas palinuri urae Newman, 1960 *Arcoscalpellum multicostatum* Newman & Ross, 1971 [accepted as *Weltnerium multicostatum*]
Lithoglyptes spinatus Tomlinson & Newman, 1960 *Arcoscalpellum utinomi* Newman & Ross, 1971
[accepted as *Auritoglyptes bicornis* (Aurivillius, 1892)] *Neoscalpellum eltaninae* Newman & Ross, 1971
Octolasmis indubia Newman, 1961 *Neoscalpellum schizoplacinum* Newman & Ross, 1971
Heteralepas mystacophora Newman, 1964
Megalasma elegans Newman, 1964
Tetrachthamalus Newman, 1967
Cyprilepadidae Newman, Zullo & Withers, 1969
Tetrachthamalus obliteratus Newman, 1967
Weltneria hessleri Newman, 1971
Bathylasmatidae Newman & Ross, 1971
Bathylasmatinae Newman & Ross, 1971
Bathylasma Newman & Ross, 1971
Abathescalpellum Newman & Ross, 1971
Annandaleum Newman & Ross, 1971
Australscalpellum Newman & Ross, 1971
Australscalpellum schizmatoplacinum Newman & Ross, 1971
Brochia Newman & Ross, 1971
Brochia bulata Newman & Ross, 1971
Gymnoscalpellum Newman & Ross, 1971
Gymnoscalpellum tarasovi Newman & Ross, 1971
Litoscalpellum Newman & Ross, 1971
Litoscalpellum fissicarinatum Newman & Ross, 1971
[accepted as *Litoscalpellum korokevitshae* (Zevina, 1968)]
Litoscalpellum simplex Newman & Ross, 1971
Litoscalpellum walleni Newman & Ross, 1971
Tetrachaelasma Newman & Ross, 1971
Tetrachaelasma southwardi Newman & Ross, 1971
Arcoscalpellum acicularum Newman & Ross, 1971
Arcoscalpellum buccinum Newman & Ross, 1971
[accepted as *Amigdoscalpellum costellatum* Hiroa Ross & Newman, 1973]
Withersia (Withers, 1935)]
Tessarelasma southwardi Newman & Ross, 1971
Cryptophialus tomlinsoni Newman & Ross, 1971
[accepted as *Australophialus tomlinsoni*]
Aptolasma Newman & Ross, 1971 [accepted as *Hexelasma* Hoek, 1913]
Aptolasma brintoni Newman & Ross, 1971 [accepted as *Hexelasma brintoni*]
Aptolasma leptoderma Newman & Ross, 1971
[accepted as *Hexelasma leptoderma*]
Aptolasma triderma Newman & Ross, 1971 [accepted as *Hexelasma triderma*]
Hexelasma fosteri Newman & Ross, 1971 [accepted as *Mesolasma fosteri*]
Oxynaspis rossi Newman, 1972
Arcoscalpellum elegantissimum Rao & Newman, 1972 [accepted as *Trianguloscalpellum elegantissimum*]
Arcoscalpellum radiatum Rao & Newman, 1972
Arcoscalpellum rossi Rao & Newman, 1972 [accepted as *Catherinum rossi*]
Altiverruca allisoni Rao & Newman, 1972 [accepted as *Cristallinaverruca allisoni*]
Cantellius Ross & Newman, 1973
Cantellius octavus Ross & Newman, 1973
Cantellius quintus Ross & Newman, 1973
Creusia decima Ross & Newman, 1973 [accepted as *Galkinius decima*]
Hiroa Ross & Newman, 1973

Hiroa stubbingsi Ross & Newman, 1973
Hoekia Ross & Newman, 1973
Synagoga sandersi Newman, 1974 [accepted as
Waginella sandersi]
Weltneria exargilla Newman, 1974
Ceratoconcha conicocystata Newman & Ladd, 1974
Ceratoconcha creusiooides Newman & Ladd, 1974
Ceratoconcha jingi Newman & Ladd, 1974
Ceratoconcha minuta Newman & Ladd, 1974
Ceratoconcha quadratoradiata Newman & Ladd,
1974
Eoceratoconcha Newman & Ladd, 1974
Eoceratoconcha kugleri Newman & Ladd, 1974
Eoceratoconcha renzi Newman & Ladd, 1974
Pagurolepas atlantica Keeley & Newman, 1974
Balanomorphoidea Newman & Ross, 1976 [accepted
as *Coronuloidea* Leach, 1817]
Archaeobalanidae Newman & Ross, 1976
Archaeobalaninae Newman & Ross, 1976
Austrobalanidae Newman & Ross, 1976
Austrobalaninae Newman & Ross, 1976
Platylepadidae Newman & Ross, 1976
Platylepadinae Newman & Ross, 1976
Bosciinae Newman & Ross, 1976 [accepted as *Mega-*
trematinae Holthuis, 1982]
Ceratoconchinae Newman & Ross, 1976
Euraphiinae Newman & Ross, 1976
Hexelasmatinae Newman & Ross, 1976
Semibalaninae Newman & Ross, 1976
Tetraclitellinae Newman & Ross, 1976
Notobalanus Newman & Ross, 1976
Tesseropora atlantica Newman & Ross, 1976
Austromegabalanus Newman, 1979
Austromegabalanus zulloi Newman, 1979
Notomegabalanus hennigi Newman, 1979 [accepted
as *Porobalanus hennigi*]
Notomegabalanus tubulatoides Newman, 1979
[accepted as *Fosterella tubulatoides*]
Neolepas Newman, 1979
Notomegabalanus Newman, 1979
Neolepas zevinae Newman, 1979
Aurivillialepas Newman, 1980
Aurivillialepas arnaudi Newman, 1980
Gruvelialepas Newman, 1980
Scillaelepas bocquetae Newman, 1980 [accepted as
Aurivillialepas bocquetae]
Scillaelepas fosteri Newman, 1980
Arossia Newman, 1982
Arossia hemryae Newman, 1982
Concavus Newman, 1982
Menesiniella Newman, 1982
Balanus cantelli Newman, 1982

Lithoglyptes tectoscrobis Grygier & Newman, 1985
Lithoglyptes viatrix Grygier & Newman, 1985
Weltneria griggi Grygier & Newman, 1985
Weltneria ligamenta Grygier & Newman, 1985
Heteralepadomorpha Newman, 1987
Praelepadomorpha Newman, 1987
Nesochthamalus Foster & Newman, 1987
Notochthamalus Foster & Newman, 1987
Rehderella Foster & Newman, 1987
Euraphia devaneyi Foster & Newman, 1987
Notochthamalinae Foster & Newman, 1987
Neoverrucidae Newman, 1989 in Hessler & Newman,
1989
Neoverruca Newman, 1989 in Hessler & Newman,
1989
Neoverruca brachylepadoformis Newman, 1989 in
Hessler & Newman, 1989
Proverrucidae Newman, 1989 in Hessler & Newman,
1989
Rugilepas Grygier & Newman, 1991
Rugilepas pearsei Grygier & Newman, 1991
Microlepas echinotrichae Grygier & Newman, 1991
Neobrachylepadidae Newman & Yamaguchi, 1995
Neobrachylepas Newman & Yamaguchi, 1995
Neobrachylepas relicta Newman & Yamaguchi, 1995
Ahoekia Ross & Newman, 1995
Ahoekia chuangi Ross & Newman, 1995
Ahoekia tanabensis Ross & Newman, 1995
Eohoekia Ross & Newman, 1995
Eohoekia chaos Ross & Newman, 1995
Eohoekia nyx Ross & Newman, 1995
Galkinia Ross & Newman, 1995 [accepted as
Galkinius Perreault, 2014]
Hoekinii Ross & Newman, 1995
Hoekia fornix Ross & Newman, 1995
Hoekia mortensi Ross & Newman, 1995
Parahoekia Ross & Newman, 1995
Parahoekia aster Ross & Newman, 1995
Pyrgopsellini Ross & Newman, 1995
Zeugmatolepadidae Newman, 1996
Zeugmatolepadinae Newman, 1996
Bryozobiinae Ross & Newman, 1996
Bryozobia Ross & Newman, 1996
Bryozobia synaptos Ross & Newman, 1996
Zulloa Ross & Newman, 1996
Zulloa imperialensis Ross & Newman, 1996
Eochionelasmus paquensis Yamaguchi & Newman,
1997
Eochionelasmus ohtai manusensis Yamaguchi &
Newman, 1997
Vertebroscalpellum Newman & Ross, 1998
Vertebroscalpellum spinum Newman & Ross, 1998

Cionophora Ross & Newman, 1999 [accepted as *Cionophorus*]
Cionophora soongi Ross & Newman, 1999 [accepted as *Cionophorus soongi*]
Imbricaverruca Newman, 2000
Imbricaverruca yamaguchi Newman, 2000
Australhoekia Ross & Newman, 2000
Australhoekia cardenae Ross & Newman, 2000
Waikalasmatidae Ross & Newman, 2001
Catolasmus Ross & Newman, 2001
Cionophorus Ross & Newman, 2001
Cionophora guillaumae Achituv & Newman, 2002
[accepted as *Cionophorus guillaumae*]
Neopyrgoma Ross & Newman, 2002
Priscansermarinidae Newman, 2004
Heteralepas cantelli Buhl-Mortensen & Newman, 2004
Neolepadidae Yamaguchi, Newman & Hashimoto, 2004
Neolepadinae Yamaguchi, Newman & Hashimoto, 2004
Neolepadini Yamaguchi, Newman & Hashimoto, 2004
Ashinkailepadini Yamaguchi, Newman & Hashimoto, 2004
Ashinkailepas Yamaguchi, Newman & Hashimoto, 2004
Ashinkailepas *sepiophila* Yamaguchi, Newman & Hashimoto, 2004
Auritoglyptes Kolbasov & Newman, 2005
Armatoglyptes thomasi Kolbasov & Newman, 2005
[accepted as *Balanodytes thomasi*]
Chaetolepadinae Buckeridge & Newman, 2006
Chaetolepas calcitergum Buckeridge & Newman, 2006
Chitinolepas Buckeridge & Newman, 2006
Chitinolepas spiritsensis Buckeridge & Newman, 2006
Cyprilepadiformes Buckeridge & Newman, 2006
Idioiblidae Buckeridge & Newman, 2006
Idioiblinae Buckeridge & Newman, 2006
Idioibla Buckeridge & Newman, 2006
Iblomorpha Buckeridge & Newman, 2006
Ibliformes Buckeridge & Newman, 2006
Lepadiformes Buckeridge & Newman, 2006
Neoiblinae Buckeridge & Newman, 2006
Neoibla Buckeridge & Newman, 2006
Scalpelliformes Buckeridge & Newman, 2006
Cryptophialida Kolbasov, Newman & Høeg, 2009
Lithoglyptida Kolbasov, Newman & Høeg, 2009
Protelminius Buckeridge & Newman, 2010
Eoatria Van Syoc & Newman, 2010
Eoatria goslineri Van Syoc & Newman, 2010
Microporatria Van Syoc & Newman, 2010
Microporatria loreleyae Van Syoc & Newman, 2010
Multatria Van Syoc & Newman, 2010
Poratria Van Syoc & Newman, 2010
Poratria monopora Van Syoc & Newman, 2010
Poratria williamsi Van Syoc & Newman, 2010
Protochelonibiinae Harzhauser & Newman, 2011
Protochelonibia Harzhauser & Newman, 2011
Protochelonibia submersa Harzhauser & Newman, 2011
Atetrapachylasma Newman & Jones, 2011
Atetrapachylasma dijonesae Newman & Jones, 2011
Zevinaella Shalaeva & Newman, 2016
Zevinaella volentis Shalaeva & Newman, 2016
Synagoga grygieri Kolbasov & Newman, 2018

APPENDIX 3

Patronyms

Our designation of an accepted current name (as of February 2021) reflects its status in the World Register of Marine Species (<<http://www.marinespecies.org/>>), accept as noted.

Abyssotrophon newmani Houart, Vermeij & Wiedrick, 2019

Acasta newmani Van Syoc & Winther, 1999

Arossia newmani Zullo, 1992

Chthamalus newmani Chan, 2016

Cryptophialus newmani Tomlinson, 1969

Epibrachylepas newmani Gale, 2014

Heteralepas newmani Buhl-Mortensen & Mifsud, 2017

Mesolasma newmani Buckeridge, 1983

Neocandona newmani Karanovic, 2005 [accepted as *Areacandona newmani* (Karanovic, 2005)]

Newmanella Ross, 1969

Newmanellinae Ross & Perreault, 1999

Newmania Anderson, 1992 [genus name is preoccupied, accepted as *Wanella* Anderson, 1993]

Newmanilepas Zevina & Yakhontova, 1987

Newmaniverruca Young, 1998

Paracalanica newmani Rosell, 1981

Utinomia newmani Tomlinson, 1963 [accepted as *Welternia hirsuta* (Tomlinson, 1963); see Tomlinson, 1969]

Wanella Anderson, 1993

APPENDIX 4

Remembrances

Yair Achituv. Bill was a collaborator and a friend. He hosted me at Scripps, which was a shrine of cirripedology where I met many pilgrims. Our joint paper on Hiroa led me to study host specificity in coral barnacles. I use at least once a week his 1976 catalog on the Balanomorpha and his 1973 revision on the Pyrgomatidae. The last one was a change of concept in the study of coral barnacles, changing Darwin's single genus *Pyrgoma* to a series of genera.

Ray Bauer. Bill Newman was a great doctoral adviser. During my first courses at Scripps, all students, no matter their concentration, took a coterie of courses in basic marine science. Bill was one of the lecturers in the Marine Organisms course, and I really looked forwards to his lectures, always with a buildup of interesting information that led up to a grand climax. After a few months, other students were finding their place with various professors and labs. However, I was a bit lost, a student from the Midwest who had only seen the ocean once before arriving at SIO. Given his great lectures on invertebrates, I went to see him and ask for advice. He had me do a special projects course with him which involved sampling and identifying the fauna from the local intertidal habitats. He set me up in the Invertebrate Collections laboratory with the microscopes and lab supplies I needed. I loved that field and museum lab experience; besides getting to know the remarkable intertidal fauna of southern California, I came upon the critters that really excited me and which I then worked with for my doctorate and for the rest of my career (shrimps!). Bill never forced his own research interests on his students, who worked with invertebrates such as shrimps, crabs, corals, chitons and (of course) barnacles. He was not a "helicopter" adviser who hovered over his student's research. He would make suggestions and was always ready with advice when asked. With Bill, we had the freedom to follow our interests wherever they led (as long as they were fruitful!). This gave his students the independence to pursue research that served well in future careers. Bill did not insert himself in our personal lives, but if we ran into trouble, he was there to

support us. He rescued two students (at least) who had gotten into some minor trouble with the law. Once I was hitch-hiking to SIO and a young policeman offered me a ride. As we neared SIO, he got a call and told me sorry, I had to get out of the car so that he could respond. Bill was a few cars behind, and when he saw me get out of the police car, he frantically called me over, asked me if I was in trouble and of course gave me a ride the rest of the way. His support during my journey to a final tenure-track position is something I will always treasure. I feel very fortunate and proud that Bill was my major professor!

John Buckeridge. I first met Bill in the mid 1970s at a Marine Biology Symposium whilst I was a doctoral student studying fossil barnacles. He had recently published the Cirripedia section in the prestigious Treatise of Invertebrate Paleontology, so he already had a formidable reputation in barnacle research. At our first meeting, he strongly challenged the way in which I understood barnacle distribution — in space and in time. He offered a fresh perspective, but did so in a way that was always constructive; his generosity of spirit and his thoughtfulness shone through and we soon became close friends. In the decades that followed, I had many opportunities to spend “barnacle time” with Bill (and Lynn) at La Jolla, often accompanied by my wife, June. Bill had an uncanny knack of blending good science with those other good things in life: food, wine, music and friendship. I cannot state just how much I miss his gentle mentoring and his camaraderie, which more than often led to a useful joint paper.

Lene Buhl-Mortensen. He was a dear friend, colleague, and mentor with whom I appreciated being able to discuss my findings. I was also fortunate to work together with Bill benefitting from his fabulous knowledge. Bill was a very generous and friendly person and I had the pleasure of visiting him and his lovely wife in their beautiful home several times.

Jim Carlton. I first heard the name William Newman in 1964, through a rather round-about route. The year before I had collected and studied a shrimp in San Francisco Bay (in an estuarine lagoon, known as Lake Merritt, in the city of Oakland) that did not appear to be in the local guides and texts available to me. Zoologists at the California Academy of Sciences in San Francisco suggested that I send my specimens to John Yaldwyn at the Australian Museum, who kindly agreed to look at them. Some weeks later back came the identification: it was the Asian shrimp *Palaemon macrodactylus*, about which, Dr. Yaldwyn informed me, a paper announcing its introduction to San Francisco Bay had just been published (Newman, 1963). As I was only 16 years old and in high school, it would take me another couple of years before I was able to locate a journal called *Crustaceana* and make a photocopy of Bill’s paper. My old-fashioned typewriter correspondence with Bill began around 1975, on the occasion of Bill working on the barnacle chapter for Light’s Manual, but it wasn’t until November 1977 that I finally made my way to Scripps to meet Bill, as well as Arnold Ross. Our email correspondence began 20 years later in 1997, and I have carefully kept as well the entire archive of these 23 years of emails — a treasure trove of observations on the systematics, ecology, and biogeography of world-wide barnacles. Nearly 50 years after my first finding it in Lake Merritt, the arrival and establishment of *Palaemon macrodactylus* in New York City was announced in 2010; I soon realized it was also in fact near my lab in Mystic, Connecticut. I wrote to Bill about it. He immediately recalled the details of its discovery in the 1950s in San Francisco Bay, followed with “It’s astonishing to me — a sedentary animal like a tunicate, sponge, mud crab or barnacle (getting around the world by ships) okay, but such a high-strung crustacean being so adaptable, withstanding Australia and Europe and elsewhere, is a big surprise to me! Ye gads, ain’t zoology grand!”

Benny Chan. I started my Ph.D. in barnacle taxonomy in 1996 and read many of Bill’s papers to learn the basics of barnacles. At that time, pdf, emails, websites and internet were not common and scientific papers were only available based on photocopied versions, and it was impossible to

expect what Bill looked like. One of Bill's key papers, co-authored with the late Arnold Ross, and one of the most important foundation paper in barnacle biology was his 1976 "Revision of the Balanomorph barnacles; including a catalog of the species." But I could only obtain it as a photocopy borrowed from Di Jones. In 1998, I attended the conference of the Western Society of Naturalists in San Diego, California. There were some Scripps colleagues at the meeting to bring conference participants to visit SIO. I was so lucky to meet Bill and Arnold at Scripps, and when I saw Bill in person, I said in my heart "Oh, there is the famous Newman I have never met, and I can talk to him now!" After we talked, Bill and Arnold gave me a signed original copy of Newman and Ross as a souvenir. It remains a precious treasure for me. I have kept all of Bill's email communications, which are rich with many important research insights and teachings.

Alberto Collareta. I never met Bill by person, but from spring 2019 to the end of 2020 we have been in very constant, fruitful and very friendly contact via e-mail exchanges. As Benny did, I also made a point of preserving all of the messages of Bill's in my e-mail box. By largely building upon Bill's corpus of research, our past and future cirripedological works will durably testify to his extraordinary stature as a scientist whose life-long quest for knowledge has been (and will always be) exemplary. In other words, Bill will keep on outfoxing us for a long, long time! I learned the word "outfoxing" from Bill, and I think it fits very well Bill's crisp, curious, and eager intellect.

Mark J. Grygier. I entered the Ph.D. program at SIO without any pre-ordained affiliation to a particular laboratory or professor. After brief exposure to neustonic insects and deep-sea meiobenthos, but still searching for a research subject more zoological than ecological, I approached Bill Newman. Opening a specimen cabinet, he showed me several bottles of "ascothoracicans", one species of which he had described a few years earlier as *Synagoga sandersi*. Since the age of 12 or so, I had been reading all the standard invertebrate texts and many other marine biological works and thought I "knew invertebrates", but I had never heard of "ascothoracicans". This was, therefore, the group for me; significant findings seemed assured for animals so little known to zoologists, and so it proved. Bill introduced me to the core literature on the Ascothoracida (this non-barnacle group's proper name), instructed me in the fundamentals of microscopy and drawing, arranged for my travel to Hawaii to collect live animals, and helped me make the proper contacts worldwide for amassing additional specimens, publishing my work, and later obtaining postdoctoral sponsorships. By the time of my thesis defense in 1984 he had overseen my production of 18 papers, either published or in press, on the taxonomy, phylogenetic significance, and other aspects of the Ascothoracida (the thesis itself was the basis of several more). Most unusually for a major professor, he did not insist on co-authorship of any of these works, since he had not personally had a hand in conducting the research and the papers did not pertain to barnacles per se. Nonetheless, we did collaborate twice, on coral-dwelling acrothoracican boring barnacles while I was still a student and echinoid-associated stalked barnacles some years later. Bill's hands-off style of dealing with students may not have been to the benefit of all of them, but in my case it was enough to get me established as a potentially major figure in carcinology by the time I graduated and began job-seeking, and for that I shall be eternally grateful.

Jens Thorvald Høeg. Bill Newman was a critical person for my career in many respects. In 1977 I had started on a project to unravel the details of host infection in parasitic barnacles (Rhizocephala). But after a year of hard work in Denmark and Sweden nothing worked. I got larvae, oh yes, but they either died prematurely or refused to settle. So, Professor Nick Holland from Scripps witnessed my efforts and said: "Jens, I know Newman had a PhD student who sadly died a year ago. He managed to culture the whole life cycle of a local species. I know it can work, so get a grant and write to Newman and come do it with us". I in fact already had some notes from

this student in hand via my supervisor and so wrote a grant proposal that covered only the cheapest possible ticket. Got the grant, packed a single suitcase with mostly larval culture gear and a few spare clothes and came to SIO. Here Bill welcomed me with open arms and opened the drawers with all the original files compiled by the student Larry Ritchie. During my two months visit I got so many results I still work with them to this day. And Newman said: "Jens, why don't you write up Ritchie's unfinished little review paper into a proper manuscript and publish it with him posthumously?" So it happened that one of my best "selling papers" (still my no. 5 or 6 most-cited) came out in the first volume of the *Journal of Crustacean Biology* even before I got my MSc degree! Thanks to Bill's generosity and support! That paper (Ritchie and Hoeg 1981, *JCB* 1: 334-347*) immediately established me among scientist peers, and the results even appeared in textbooks such as Barnes' *Invertebrate Zoology*. And did Bill Newman ask to be co-author? No such thing! Those were the days when mentors and supervisors gave you "opportunity". They may not have meddled or assisted much in your lab work or interpretations, but nor did they claim credit for more than being exactly "your mentor".

And so started a long lasting relationship and friendship with Bill. Some years later I again worked at SIO, and now actually within his lab. And at this visit and several to come, I always stayed a few days at his and Lynn's beautiful La Jolla home. Here I learned how Bill's days operated:

At the lab around 9am. Car parked in the upper car park (salt will destroy it on the parking lot lower down!). Work until a brief stand up for morning coffee. Work again until a brief brown bag lunch out on the green overlooking the Pacific. More work, more coffee, and then home by around 5 or 5.30 pm. In the office the blinds were down: the afternoon sun and beautiful view of the Pacific would spoil the computer image and work discipline! At home, I do not think Bill did much science if at all. You could discuss it alright, but no reading or writing. He was dedicated to his garden and green house and aquaria and spent many hours tending to them as the highly skilled craftsman he also was. And then, for dinner, copious amounts of wine in his privately labelled bottles and then we must not forget that he could have been a superb bartender: His cocktails bore witness to that.

One thing that Bill rarely mentioned was that one of his sons, James H. Newman, is a famous shuttle astronaut. He was part of one of the HUBBLE servicing missions in 2002, experiencing another one of those fantastic EVAs (space walks). From Bill, I got the rare privilege of having the email address of a NASA astronaut, and so exchanged a few emails with James (I have been a space buff for many years). I came to know this first only by way of the Hollands – Bill never mentioned it to me earlier!

A few more fond memories:

In 1988 during one of my few "not being funded spells" Bill passed through Copenhagen (on his way to the USSR) and wanted to cheer me up. We agreed to meet at the Town Hall Square and Bill said, "Let's go for beers". We found the "Queens Pub", a hotel-associated pub which was and is about the most expensive place in an expensive part of Copenhagen. I said cautiously, "Perhaps it would be better to find a cheaper place"; "No," said Bill, "I'll cover the bill, this looks just fine." Which indeed it was and after several large beers and covering everything across the Thecostraca, we had to part and Bill called for the bill. Here came the smiling waiter: Bill looked at the bill and said, "Can this be right?" The waiter said, "Oh yes, Copenhagen is an expensive city!" I said, "Bill, I told you so!" Bill left somewhat in a daze, less from the beers than from the shock! I can say in honest truth that Bill never ever forgot those beers — not that he regretted it or anything, only "that bill!"

In 2009 he was an invited keynote speaker to the joint TCS-CSJ meeting in Tokyo, but poor health prevented him from fulfilling that obligation, although indeed he did attend the meeting. I suppose his wife Lynn had said: You can go, but no seminar! So I was invited to do the job (I was confident, given Bill's recommendation). Having given the talk, Bill came up to me and shook my hands saying: "Jens, this is probably the best talk I have ever heard". That surely warmed my heart as only true praise from a beloved mentor can do.

Then in 2014 I had the honour of receiving the TCS Research Excellence Prize at a Society of Integrative Biology meeting in Austin, Texas. Sadly, rather few carcinologists now turned up at these important meetings. But who turned up among the few people gathered for the Prize event in the late afternoon? — Bill Newman, who never attended many meetings at all! But for this one he flew in from San Diego, staying for a night, solely to be part of the event! Such was Bill Newman: generous, scientifically open and the most hospitable of hosts in both lab and at home. This despite the many furious discussions we had over scientific problems. Often, during a visit, they played out "the olde way", over a little blackboard close to the coffee machine! Many were the disputes and on many we remained in disagreement, but it only rarely spoiled the pleasure and the good will between us! And if so, not for long!

*) Subsequently, Bill sent me all of Larry Ritchie's files – a very extensive set of data and notes covering research from 1972-1977 on the local rhizocephalan *Lernaeodiscus porcellanae* and its host crab *Petrolisthes cabrilloi*. Those files are still with me and combined with my own results they led to more papers with Ritchie co-authoring, and several more where these files played an important part of the underlying dataset.

Diana Jones. In 1993, whilst working on *Uca* in Michel Turkay's laboratory in Frankfurt, I couldn't resist looking at their barnacle collection, as I had developed a keen interest in these fascinating creatures. I was very excited to come across some hydrothermal vent specimens of *Neolepas* from the vicinity of Easter Island. Bill had described the first hydrothermal vent barnacle, *Neolepas zevinae*, in 1979 from the East Pacific Rise, and so I contacted him, to see if he would like them sent to him. He replied saying "you can do it, get on and describe them!" This generous gesture and Bill's continued mentoring and interest since that time have ensured my enduring fascination with barnacles, as well as engendering my own willingness to mentor younger cirripede researchers to be as enthralled as I am, and as he was, by them. Sadly, I only physically met Bill once, at the 1990 International Crustacean Society Conference in Brisbane, but have fond memories of him mischievously encouraging Toshi Yamaguchi to waltz me round the dance floor at a dizzying pace and, as I am short and Toshi tall, my feet were often not on the floor! We have lost and will sorely miss our amazing friend, colleague and champion.

Francis Kerckhof. I was delighted and honored when Bill – the eminence grise of the barnacle lovers – approached me about 10 years ago with some questions, illustrative of Bills curiosity, dealing with old (17th-18th) Dutch publications that depicted barnacles and barnacle larvae, without knowing at that time that they were barnacle larvae of course. So, we dived into some detail, and, to cite Bill "at home, but in looking over my queries below I see that, as sometimes happens, in being intent on I's to dot and T's to cross, one forgets the central question!" — an attitude that FK recognizes all too well. We had a nice and fruitful correspondence and exchange of thoughts, wondering why it took so long before barnacles were recognized as crustaceans, and more.

Tomas Koci. Unfortunately, I did not have the chance to meet Bill personally, but we communicated via email from circa 2013, doing so on a broad range of topics, such as Cretaceous sessile barnacles; scalpellids such as *Smilium*, *Euscalpellum*, *Stramentum*; on the origin of sessile barnacles; phosphatization of eolepadid cirripedes; on acrothoracid cirripedes – *Trypetesa*, *Lithoglyptes*,

and *Weltneria*; on continental drift, biogeography of barnacles and other topics, including his travels in California, Spitzbergen and Europe. I remember him as an inspirational man with an “open mind”, always ready to help me in my scientific endeavors. Bill was a good “brother in arms” and a fair “warrior” with a keen sense of humor.

Jorge Laguna. Bill Newman was my mentor and we stayed in touch for many years. He had a good sense of humor and I had the honor of sharing the lab with him and eating delicious meals with him and his wife Lynn. Bill was the first one at his lab and the last one to leave and we spent countless hours talking about his passion for biogeography, plate tectonics, and systematics. He encouraged and supported me on my studies on Tropical Eastern Pacific Biogeography and on my paper on *Euraphia eastropacensis*. Bill said that he wasn’t only teaching me about Cirripedia, but was preparing me for life in order for me to apply my training to ANY future endeavors. Bill was right about that.

Ray T. Perreault. I met Bill Newman in person in March, 1996. We had been communicating by mail for a couple of years, and I made San Diego part of a vacation to Washington for fossil collecting. I spent two nights as his and Lynn’s house guest and a very productive day at his lab. I also met Paulo Young and Arnold Ross there. All of us conferred together in the lab, and at the end of the day, I made a scraping collection from Scripps pier, which was close to Bill’s lab. The second night’s supper was quite grand, with Paulo and Arnold attending. I had brought along some strange fossil and modern barnacles to discuss. Arnold Ross recognized one as an undescribed *Newmanella* which resulted in a paper describing it and partial revision of tetraclitellines. Altogether, a highly enjoyable and profitable leaning experience. Like others in Bill’s association, I have kept all of our paper and electronic correspondence. Looking over my own publications, I find that every one has benefited from his advice and insights, and my present research projects have also done likewise. I shall miss Bill Newman.

Fabio Pitombo. I had a chance to do a field trip with Bill in the Colorado Delta, in 2001. We traveled all day searching for barnacles in small creeks and ponds, until we found them on a last try in a drainage channel. During the trip we had a chance to chat on a variety of subjects including our mutual appreciation of Darwin’s work on barnacles. Later, back in San Diego, moved by my appreciation of Darwin’s work on barnacles, he gave me his Darwin volume of living lepadids. At that time, I didn’t grasp the magnitude of his offer, but now it is clear that it was a way to encourage and inspire me. The last time I visited him, in 2015, he was still in the same spirit, with a sharp mind and many questions on barnacles. I’ll miss him as a mentor and friend and, as I witnessed in the Colorado Delta twenty years ago, his passion for barnacles.

Alireza Sari. My PhD supervisor the late Dr. John Moyse recommended reading the chapter by Bill in Treatise on Invertebrate Paleontology, which was the first valuable and informative one on barnacles I read in 1993. After reading this professionally written chapter, it was a dream for me to see him one day in a conference. Luckily, I visited Bill for a day in the summer of 2012 and I was amazed at his generous welcome at his office, lab, and later his and Lynn’s hospitality at home to discuss the matter about presence of the exotic species *Amphibalanus subalbidus* in the Persian Gulf. He precisely dissected and made a cross section of a tiny scutum using grinding wheel to see the minute internal spaces within calcified plate. Then, he verified the early identification of the material, which was possible using this discriminative character by his self-made quick method. For several years we have discussed matters of interest on barnacles — and even on hurricane formation. We lost a great encouraging mentor who always responded promptly to my students and me.

Eve Southward. I was with my late husband Alan on his travels in North America in 1963, when we first met Bill Newman at Scripps and he introduced us to the shores of Baja California,

Mexico. I remember Bill's sabbatical of a few months in 1973 at the Marine Biological Association in Plymouth, England, when he had peace and quiet to settle down quietly with his typewriter to prepare publications of his own recent work. Much later, in 1978, Bill organized the great Tropical Eastern Pacific Expedition (TEPE) on board the R V *Alpha Helix*, cruising from the Panama Canal western exit north along the Pacific coast of central America, on the way back to San Diego, California (see Laguna 1990 Bulletin of Marine Science 46: 406-424). The ship dropped off groups of scientists for a few hours each time at numerous interesting coastal sites along the way, and the expedition included some offshore dredging and subaqua collecting. Thanks to Bill, the ship's officers and the SIO management, this international cooperative effort moved effortlessly and successfully. I still have many of our TEPE barnacle specimens, photographs and notes, my own drawings and pleasant memories of places and people.

Jon Standing. Bill was a giant in cirripedology — a *Balanus nubilus* in a sea of barnacles. Although I met him personally only several times, we corresponded for a number of years. In those letters, he was always encouraging. He read the manuscript for my first cyprid article, offering some wonderful insights and edits, and he probably refereed some of my later papers. In short, he was a great mentor for young barnacle biologists, perhaps in the same tradition that so many of us experienced in Invertebrate Zoology at the University of California at Berkeley.

Bob Van Syoc. As a student of Bill's in the late 1980s and early 90s I appreciated his open door policy as an advisor. He welcomed me into his office to talk about my research and many other topics. His knowledge of ocean science and evolution ran deep and he shared it freely with me. One of the things we talked about was the various growth forms of barnacles and how their opercular plate shape might change with density. Bill had made some wooden racks with glass plates that we submerged into the Salton Sea and within a week they were covered with newly settled *Amphibalanus amphitrite*. My plan was to selectively remove individuals from the plates as their shell growth impacted their neighbors, but I needed a good place to hang the racks where the barnacles could feed and grow. To my surprise, Bill suggested that I hang barnacle covered racks off the side of his boat in San Diego harbor! I'm sure there is not another boat owner in the world that would welcome barnacles around their boat, but Bill did. The experiment went well and resulted in a meeting presentation and a publication (Van Syoc, 1992, Proc. San Diego Soc. Nat. Hist. 12:1-7. Thanks Bill!

John Wares. Bill's energy towards barnacle biology was, in fact, contagious. In the 1990s, as a young graduate student only recently trained in invertebrate biology, I needed some assistance learning how to dissect and evaluate the internal traits of chthamalid barnacles and wrote Bill an email. That email began nearly 25 years of regular correspondence, including a live mussel covered in barnacles shipped across the country in newspaper via first class postage, alert grumblings about my confusion in using informal taxonomy in my first publication, an invitation to give my first professional talk at Scripps (where I recall him drinking from a coffee mug partly encrusted in barnacles), lessons on proper use of Latin in species names, observation-rich thoughts on bio-geography, kind critiques of my reports on barnacle diversity, and more. His attention to my work and persistent collegiality seems to be something he spread to so many other colleagues, and even in the past year I have been working towards answering a question he was still pondering. I consider Bill one of my true mentors although we only met face-to-face a few times.

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